

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NO. 2

A CONTRIBUTION TOWARD AN
ENCYCLOPEDIA OF INSECT
ANATOMY

By
ROBERT E. SNODGRASS
Late Honorary Research Associate
Smithsonian Institution



(PUBLICATION 4544)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JULY 12, 1963

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NO. 2

A CONTRIBUTION TOWARD AN
ENCYCLOPEDIA OF INSECT
ANATOMY

By
ROBERT E. SNODGRASS

Late Honorary Research Associate
Smithsonian Institution



(PUBLICATION 4544)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JULY 12, 1963

21
575
542

PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

FOREWORD

At the time of his sudden death, on September 4, 1962, Robert E. Snodgrass was working on a book we might call "An Encyclopedia of Insect Anatomy." His notes and correspondence suggest several possible titles, but this one seems most appropriate for the material. To judge from the list of terms he had compiled for the letters A to D, I would estimate that the work was only somewhere between 10 and 20 percent completed. Most manuscripts would be unsalvageable when in such an early stage, but this one need not be thrown away. An encyclopedia may be considered as a dictionary in which definitions of maximum brevity are replaced by essays on the various terms. In this sense, each of the essays Dr. Snodgrass had written may be considered as complete—the work is incomplete only in the sense that he had progressed only a short way down the list of projected essays. Hence the title chosen for this publication.

In consultation with Mrs. Snodgrass and others it was decided not to attempt completing the work, because who besides Snodgrass could write Snodgrass's Encyclopedia? The essays are published almost word for word from the original manuscript. However, this was preliminary manuscript which did require some editorial emendations. No doubt, if he had lived, he would have done more revision—such was his habit—but I have kept changes to a minimum in order not to alter the author's meaning. Actually he had already done some rewriting, as shown by the fact that there were three versions of "Metamorphosis," two of "Pleuron," etc. In such cases the most extensive version is used here; in some cases additions to it are taken from the less extensive versions. No attempt was made to make the several essays stylistically consistent with one another; thus some begin with derivation of the word and/or a definition; others do not.

I presume that if this material had been completed it would have been assembled with the terms in alphabetical order. But, although Snodgrass had an alphabetical list from A to D, he was not writing simply by going down this list in 1, 2, 3 order. Rather he was writing on series of related topics. Accordingly, in view of the limited amount that had been finished, it seemed preferable to assemble the finished articles into a natural rather than an alphabetical order. Perhaps this decision has one disadvantage. A certain degree of repe-

titiousness is inherent in a presentation of this sort in contrast to the presentation in a textbook of anatomy or morphology. To remove the repetition would require so many cross references that the utility of the compilation would be seriously curtailed. Some of the repetition has been removed during editing this manuscript, but some of it has been left in for the same reason that the author put it there in the first place. With the subject-type of arrangement, instead of alphabetical, some of the repetitions are brought together in adjacent articles where they become obvious in a way they would not have been were the manuscript complete and alphabetically arranged.

Bibliographic references are limited to those he had written into the text.

It is one of the losses to entomology that this encyclopedia was not completed by the author. But even this group of essays is a contribution. Unfortunately, it is his last contribution to entomology.

A. GLENN RICHARDS

Department of Entomology
University of Minnesota
St. Paul, Minn.

LIST OF SUBJECTS TREATED

	Page		Page
Insect, entomology, Hexapoda..	1	Alimentary canal	15
Anatomical names	1	Gastrula	17
Body segmentation	2	Gastrulation	18
Segments	3	Mesenteron	20
Segment areas and sclerotiza- tion	4	Stomodaeum and proctodaeum.	21
Segmental plates	5	Head	21
Body regions and plates.....	6	Epicranial suture	27
Tergum and notum.....	6	Ecdysial cleavage line of head..	27
Pleuron	7	Antenna	27
Sternum	8	Neck	28
External grooves of skeleton..	8	Gula	29
—Ite	9	Thorax	29
Larva	9	Spiracle	31
Pupa	11	Leg	31
Metamorphosis	12	Wings	33
Recapitulation	14	Abdomen	36
Moulting	15	Male genitalia	37
Ecdysis	15	Aedeagus	41
		Ovipositor	42

[See also INDEX, page 47]

A CONTRIBUTION TOWARD AN ENCYCLO- PEDIA OF INSECT ANATOMY

BY ROBERT E. SNODGRASS

*Late Honorary Research Associate
Smithsonian Institution*

Insect, Entomology, Hexapoda: An insect, according to the composition of its Latin name (*in* + *sectum*, cut), is literally an "incut," as it is also by its Greek name, *entomon* (*en* + *tomos*, cut). The study of insects is *entomology* instead of insectology because the latter involves a combination from two languages. When arthropods came to be named according to the number of their legs, as decapods, myriapods, centipedes, etc., the 6-legged insects became hexapods and were classed as the Hexapoda (Gr. *hexa*, six, + *pous*, *podos*, leg). Hence we call them *insects*, classify them as *Hexapoda*, call their study *entomology*, and call ourselves *entomologists* (= students of incuts).

Anatomical names: The early zoologists who first studied the anatomy of invertebrate animals naturally carried over to what appeared to be functionally corresponding organs of the latter names that were long established in vertebrate anatomy. The anatomical names of insect parts, for example, except for a few applied on a basis of analogy, are almost wholly vertebrate names. It thus came about that the same names are applied to parts and organs in vertebrates and insects that can have no possible analogy. However, our whole anatomical terminology would be thrown into confusion if homology throughout the entire Animal Kingdom were made the basis of nomenclature. When organs are named on a functional basis, the same names are applicable to a worm, an arthropod, or a vertebrate.

A food tract extending through the body, for example, is literally an alimentary canal in any animal in which it occurs. A blood-pumping organ is properly a heart regardless of its structure. An appendage for walking is a leg. A head is a head whether on an insect, a snake, a man, or a snail. An organ of flight is a wing (*pteron* or

ala) whether on an insect, a bird, a bat, an angel, the devil, or an airplane.

Of course, the early nomenclators made some mistakes in identifying organs of insects from comparison to vertebrates. For example, they called the cellular layer of the body wall below the cuticle the "hypoderm," whereas it really corresponds with the epidermis of the vertebrate. The preoral space between the mouthparts, which are modified legs, they regarded as the mouth cavity of the insect and called the food pocket over the hypopharynx, now known as the *cibarium*, the "pharynx," whereas a true pharynx is postoral and is an anterior part of the alimentary canal. Incidentally, they have left us the incongruous terms of epipharynx and hypopharynx for preoral structures which have no relation to the pharynx.

A notable misnomer in insects is the term "suture" commonly given to the grooves of the exoskeleton that form strengthening internal ridges. The word *suture* can mean only a seam (*sutura*) or line of union between adjoining parts, and undoubtedly it was suggested to the early entomologists by the sutures of the vertebrate skull. The word suture has a specific meaning that could be applied to any line of union, but cannot be made to mean anything else. It is a distortion of its meaning to apply it to a surface groove formed by inflection of the cuticle. Of course, it is only in a figurative sense that anything in anatomy may be called a suture. The only true anatomical sutures are those made by surgeons.

Another misnomer, now thoroughly established, is the application of the term *chorion* to the insect eggshell despite the fact that this shell is secreted by the ovarian follicle, whereas the vertebrate chorion is a cell layer proliferated by the embryo.

It seems better to live with these incongruities than to attempt to rectify all of them. After all, everyone has some concept of the meaning of terms such as mouth, heart, leg, etc., and the only persons likely to be concerned with the differences between, for instance, vertebrate and invertebrate hearts are those who know the differences. They will not be confused by using a term such as heart for several nonhomologous structures of different animal phyla.

Body segmentation: The primary body segments of an adult insect are the annular sections of the integument marked by the lines of attachment of the longitudinal muscles. A body segment literally should be a somite (*soma* + *ite*), but preliminary to body segmentation there are formed corresponding pairs of cavities, the coelomic sacs, in the mesoderm. Some embryologists, as Manton (1949), de-

fine the somites as the coelomic sacs and then contend that segmentation begins in the mesoderm. This usage is confusing because the true mechanical segmentation of the body results from muscle attachments to the body wall. The muscles themselves, however, are derived from the walls of the mesodermal coelomic sacs. Since the coelomic sacs are typically connected with the exterior by coelomic ducts, their primary function was probably the collection of waste products to be excreted through these ducts.

The primary segments of the body are established by the attachment of the longitudinal muscles to the cuticle. The lines of muscle attachment, as seen on the abdomen, are marked externally by transverse grooves which form internally submarginal ridges, the *antecostae*, near the anterior edges of the terga and sterna. In a soft-bodied worm or insect larva the musculature, attached at the true segmental lines, brings about a shortening of the body and allows squirming or flexing movements. In an animal with a fully sclerotized integument, however, such movements would be impossible. To give freedom of intersegmental movement, the posterior part of each segment remains membranous. The functional segments thus become the sclerotized annuli, and the connecting membranes are known as the intersegmental membranes. The definitive mechanism is thus a *secondary segmentation*.

Segments (L. *segmentum*, from *secare*, *sectum*, cut off): The term applies to body segments or *somites* and also to leg segments or *podites*.

The functional body segments are the sclerotized rings of the integument separated by flexible unsclerotized areas and movable on each other by intersegmental muscles.

The true body segments are limited by the lines of attachment of the longitudinal muscles, marked externally by grooves of the cuticle forming anterior submarginal ridges or *antecostae* of the segmental plates on which the muscles are attached. This is the *primary* body segmentation which corresponds with the musculature. The functional segments represent a *secondary* segmentation since the so-called intersegmental membranes are the posterior of the primary segments. This secondary segmentation allows the consecutive segments to be movable on each other because the connecting membranes can be infolded or extended according to the tension of the muscles. Where segments are united, as in the thorax, the membranes are either eliminated or themselves sclerotized as postnotal plates.

The leg segments are movable by muscles arising in the proximal

segment, but the segmentation becomes confusing because the segments are often divided into non-musculated subsegments. A true leg segment is thus best defined as a section of the limb provided with muscles (see Legs). In the same way the apical segment, the flagellum, of an antenna is commonly divided into subsegments (see Antennae).

Segment areas and sclerotization: In an adult insect the cuticle of each segment is usually sclerotized in a definite pattern of plates, but the pattern may differ on different segments or on the same segment in different insects. There often results, therefore, some nomenclatorial confusion on the identification of the plates.

In an unsclerotized wormlike animal, such as *Peripatus*, having a series of legs along each side of the under surface, the only differentiation of the body wall is its division by the legs into a *dorsum* above the legs and a *venter* between them. If the segmental body wall, as in some crustaceans, is completely sclerotized, the dorsal plate is a *tergum* or *notum*, the ventral plate a *sternum*. In some of the diplopods and crustaceans and in the prothorax of some insects the upper part of the tergal arch is produced on each side into a *paranotal lobe*. The sclerotized lateral parts of the segment are then called the *pleura* (sing. *pleuron*), and the name tergum or notum is restricted to the dorsal sclerotization above the lobes. In the winged insects the paranotal lobes of the mesothorax and the metathorax are extended as the wings. The pleura of these segments have to serve as supports for the wings as well as supports of the legs and are modified accordingly. Each is strengthened by a strong internal ridge formed by an external groove or sulcus from the leg base up to the wing base. The groove differentiates the pleuron into an anterior area called the *episternum* and a posterior area called the *epimeron*. At the wing base various small sclerites are formed which control the movements of the wings. Other modifications of the pleura are often present (see Pleuron), and the pleural area in wingless insects may be largely unsclerotized. The prevalent theory that a large part of the thoracic pleuron has been derived from a primitive "subcoxal segment" of the leg seems quite unnecessary from a comparative study.

In the same way as the pleuron, the tergum and the sternum are usually differentiated into areas or distinct parts for mechanical reasons.

On the abdominal segments, the terga and sterna are connected by membranes that may be regarded as pleural. But the small sclerites

sometimes found in the pleural membrane of the abdomen appear to be detached parts of tergites or sternites and hence to be laterotergites or laterosternites rather than true pleurites (see Abdomen).

Segmental plates: Sclerotization of the body wall cuticle is highly variable in different parts of the insect according to the functional requirements. On the abdomen typically the sclerotization forms a back plate or *tergum* and a ventral plate or *sternum* separated on the sides by membranous areas to allow for the movements of respiration. On the thorax the support of the wings above and the legs below necessitates the presence of a strong lateral or pleural sclerotization on each side. The head, though it includes at least four primary body segments, is continuously sclerotized above and on the sides to form a rigid cranium for the support of the antennae and the mouthparts.

Since the skeleton of each section of the insect's body is adapted to the functions of the particular part, it is difficult to deduce what the sclerotization of a primitive segment may have been. The centipedes with their undifferentiated bodies have on each segment a distinct dorsal and a ventral plate with the legs arising from flexible pleural areas between. This condition, however, is simply an adaptation to the centipede's way of locomotion and is not necessarily primitive. On the other hand, in the lower Crustacea, such as *Anaspides*, the back plates are continuous over the dorsum and down on the sides to the leg bases attached on the tergal margins. There are here no differentiated pleural plates. Among the Malacostraca, in the Mysidaceae the carapace covers only a part of the thorax, the segments behind it carry the legs on the lower margins of the terga, but where the carapace cuts through the back, the leg-carrying parts of the terga are cut off and are called pleural plates. The so-called pleural plates are here, therefore, only lateral parts of the tergal plates. Finally, in the diplopods the segments are continuous rings. It is clear, therefore, that there is no primitive basic pattern of segment sclerotization, nothing comparable to the evolution of the bony skeleton of vertebrates, among the arthropods. An original wormlike creature probably had a soft cuticle which has been variously sclerotized according to the needs in each group and according to the functional demands in each segment of the body.

The sclerotized cuticle also becomes variously reinforced by linear inflections that form strengthening ridges on the inner surface. On the external surface these appear as narrow grooves or sulci, long erroneously called "sutures" in entomological terminology. The sulci

form characteristic lines on the head; on the thorax the pleuron is braced between the wings and the legs of the wing-bearing segments by a strong ridge-forming sulcus. Elsewhere, all over the body, similar reinforcing grooves may be present. They differentiate the cuticula into areas known as sclerites, and have given the impression that the insect skeleton is composed of plates united along "sutures."

Body regions and plates: In describing the surface regions of the body or those of a body segment, we have in general three areas to distinguish and in each segment three corresponding sclerotizations. To name these we have a choice of both Latin and Greek names for the body surface regions of an animal but no names for the segmental plates on the insects. Hence the available names have been used arbitrarily to fit the needs of insect anatomy without strict regard to the primary meaning of the words.

The entire back of the insect or the back of any segment may be called the *dorsum* (L. for back), and from this we have the term *dorsal*. The back plate of a segment may then be given the name *tergum*, another Latin word for back. In the thorax, however, the Greek name *notum* is preferable in order to combine properly with the Greek prefixes *pro-*, *meso-* and *meta-* which designate the segments.

For the sides of the animal we have no technical term in common use. Since, however, *lateral* refers to direction toward the side, it is to be assumed that the side itself is the Latin *latus*. Lateral sclerotizations of the segments, when not a part of the dorsal or ventral plates, are termed the *pleura* (Gr. *pleuron*, a rib), and the pleural sclerites are properly *pleurites*.

The whole underside of the animal is appropriately the *ventral surface* from the Latin word *venter*. The Latin word, however, meant specifically the belly (also the stomach or the abdominal cavity). A segmental sclerotization of the venter is a *sternum* (Gr. *sternon*, the breast or chest), whence sternutation or sneezing.

The segmental tergal and sternal plates are often called "tergites" and "sternites." The suffix *ite*, however, means "a part of" in anatomy, as in somite or podite. It is therefore incongruous to apply *ite* terms to whole plates, and, worse, it leaves us with no terms for parts of the terga and sterna when the latter are subdivided into true *tergites* and *sternites*. (It should be noted that tergite is properly pronounced in English as tēr'-jīte.)

Tergum and notum: *Tergum* is Latin for the back of men or animals, but, since we have also the Latin word *dorsum* for the whole

back (whence the adjective *dorsal*), it is useful to restrict the term tergum to a major plate of the dorsum. Many entomologists use "tergite" for a segmental back plate, but the suffix *ite* in biology means "a part of," as in somite and podite. Properly, therefore, a *tergite* should be a division of a tergum; if the word tergite is used for the entire segmental plate we are left without a word for the parts of a subdivided tergum.

Notum is the Latinized Greek equivalent of tergum (from Gr. *noton*). It is properly used for the back plates of the thorax in combination with the Greek prefixes *pro-*, *meso-*, and *meta-*.

Pleuron: The term is derived from the Greek *pleuron*, *pleura*, a rib. The pleura in general may be defined as the lateral sclerotizations of the body segments between the tergal and sternal plates. In insects such sclerotizations are present principally on the thoracic segments and are best developed in connection with the wings.

The insect pleuron seems to have no prototype in the other arthropods. In the primitive crustacean *Anaspides* the back plates of the thoracic segments are continuous over the dorsum and down the sides, and they support the legs on their lower margins. In the Malacostraca the carapace cuts out the back of the dorsal plates, leaving the lateral parts as plates supporting the legs. These plates might be called "pleurites," but they are simply remnants of the primitive terga. The diplopods likewise have no pleural plates separate from the terga. In the chilopods, plates in the pleural region above the coxae appear to be derivatives of the coxae.

Among the insects, the pleural sclerotization of the thoracic segments is never continuous with that of the dorsum. In the Protura and Thysanura, the terga and sterna are separated by wide membranous areas. The pleural sclerotization in each segment consists only of a pair of narrow sclerites concentrically arched over the base of the coxa; these are termed the *anapleurite* and the *catapleurite*. The same type of pleural sclerotization occurs in some larvae of the lower pterygotes and in adult termites. The presence of two supra-coxal pleural arches in the thoracic segments may be regarded as a primitive condition in the insects having no relation to anything in the other arthropods.

In the pterygote insects the pleural sclerotization becomes more or less continuous over the sides of the thoracic segments but shows many modifications. Typically it is marked by a conspicuous groove, the *pleural sulcus*, extending upward from the leg base; this forms a strong ridge on the inner surface, on the lower end of which the

coxa of the leg is articulated. This sulcus and its ridge differentiate the pleuron into an anterior *episternum* and a posterior *epimeron*. Usually a triangular plate below the episternum, termed the *trochantin*, forms by its lower angle an anterior articular point for the coxa. The episternum itself may be variously subdivided, and often peripheral parts of the pleural area remain membranous. In the wing-bearing segments the pleural sulcus extends up to the wing base, and its ridge forms the fulcral support of the wing. Before the wing fulcrum there is a small plate, the *basalare*, and behind it another, the *subalare*, that give attachment to the direct muscles of the wing. The pattern of the pleural sclerotization differs on the two alate segments according to the relative development of the wings and to the presence or absence of one of the pairs of wings.

It is clear that the thoracic pleura of the pterygote insects are adaptive developments, first for the support of the legs and then for the support of the wings as the latter were evolved from paranotal lobes. It has long been a popular theory that the pleura represent primitive subcoxal segments of the legs that have been incorporated into the thoracic wall. Yet a subcoxal segment is not present in any of the other arthropod groups; the coxa is always the functional base of the limb on which the principal motor muscles of the leg are attached. Differences in the leg segmentation among the arthropods are due principally to the presence of one or two segments in the trochanteral region of the leg. Most of the arthropods have a 7-segmented leg; the insect leg is 6-segmented by loss of the second trochanter (the crustacean basipodite).

Sternum: The word is derived from the Greek *sternon*, which means the human chest or breast region. In the Latin languages the name was taken as the basis for words meaning sneezing, as in Latin *sternuto* and *sternutatio*, in Italian *sternutare*, in Spanish *estornudar*, and in Latin-English *sternutation*. In vertebrate anatomy, however, the name sternum was given to the breast bone (*os pectoris* in Latin). In arthropod anatomy it has been extended to any one of the segmental ventral plates of the skeleton. It is thus a curious coincidence that the word sternum as used in entomology is cognate with words signifying sneezing.

External grooves of skeleton: Grooves on the surface of the integument, particularly those of the head and thorax, give the skeleton the appearance of being composed of sclerites united along these lines. The grooves, therefore, have long been called "sutures"

(*L. sutura*, a seam). This was probably first suggested by the sutures in the vertebrate skull, which are formed by the coming together of bones growing out from centers of ossification. The analogy has given rise to the false impression that the insect skeleton with its "sutures" is formed by the union of parts developing from separate centers of sclerotization.

Most of the grooves of the insect skeleton are actually lines of cuticular inflection forming internal ridges to strengthen the body wall in regions of mechanical stress. They are therefore not sutures in any literal sense, and for descriptive purposes are better termed *sulci* (*L. sulcus*, a groove or furrow). The Greek equivalent *aulax* has also been used.

In a few cases grooves of the insect skeleton are lines of secondary union between sclerites. These might figuratively be called sutures.

-Ite: A suffix used in biology to denote "a part of" some larger unit, as in *somite*, *podite*, *sclerite*, etc. Very commonly it is appended to *tergum* and *sternum* giving *tergite* and *sternite* for the major plates of the body segments. This usage, however, leaves us with no terms for subdivisions of the plates which properly would be the tergites and sternites.

We encounter also the term *gonocoxite* applied to what is evidently the coxa itself. The *ite* is here clearly unnecessary. The term *coxopodite*, however, is entirely correct since it means the coxal part of a leg.

Larva: The word is derived from Latin and means a spectre, a ghost, a hobgoblin, or a mask. If we take the last meaning, a mask, a young insect is best defined as a larva if it differs so much in appearance from its parents that it must be reared to determine its identity. When a young insect resembles its parents except for the full development of wings and reproductive capacity it is called a nymph or, in some aquatic orders, a naiad. [This distinction between and retention of the terms larva and nymph is not shared by many entomologists. Most embryologists and physiologists today do not make any distinction between the two; any immature insect is called a larva.—A. G. R.]

Larvae of different species differ so much in the degree of departure from the adult form that it is evident they have undergone various degrees of evolution diverging from the parental structure. Larvae therefore can in no sense be regarded as representing ancestral adult forms of their species, nor can they be attributed to "early hatching" of the embryo—once a popular theory. We must

assume that at some time in the past history of the insects the young, as those of most other animal groups, resembled their parents except for immaturity, as does a modern young grasshopper or a young cockroach. The question then is: Why have the young of some groups departed from the parental form along their own lines of evolution? The question is not so difficult to answer as it might seem, since some larvae are very similar to the adults and others depart in varying degrees until they have lost all resemblance to the adults that produce them.

As long as the young insect can live and feed in the same environment as its parents, as the young grasshoppers and cockroaches do, there is no need of it having a special structure of its own. The adults of many insects, however, have taken advantage of their wings to explore other habitats for new sources of food, and in most cases they have been structurally modified for life on the wing and for feeding on some special kind of food. The flightless young, therefore, could not possibly keep up with their parents. So, to insure the survival of the young, nature has fitted them for a way of living and feeding of their own. The young cicada affords a very simple example of juvenile metamorphosis since it is adapted merely for burrowing in the earth. The young mayfly and stonefly are supplied with gills for an aquatic life. More extreme cases are seen in the young of Lepidoptera, Diptera, and Hymenoptera. Caterpillars are adapted for climbing and feeding on vegetation, whereas the adults fly around and usually suck nectar. The young mosquito would starve if it had to feed on blood as does its mother or on nectar as does its father. Hence it has become strictly adapted to an aquatic life and equipped with a special feeding apparatus of its own. Young muscoid flies could not live the life of their winged parents and have become transformed into maggots fitted for other ways of living. The grubs of many Hymenoptera are fitted for living in cells where they would be completely helpless if not fed by the adult.

In no case can the larva go over directly into the adult. It must at least discard its specialized larval structures, and the more it has departed from the parental form the more it has to discard. In extreme cases the larva is almost completely destroyed at the end of larval life. The modern adult represents the last stage of phylogenetic evolution of its species; the larva is a temporary specialized form of the young insect. In ontogeny the larva develops first, but it must at last give way to development of the adult. (See Pupa.)

Though the process of the destruction of the larval tissues and the resumption of imaginal development has commonly been called the

“metamorphosis” of the insect, the true metamorphosis is the change of form the larva has undergone in its independent evolution. (See Metamorphosis.)

Pupa: The term is taken over from the Latin word for young girl, puppet, baby, or doll. While there is no question as to the applicability of the word, there has been much discussion as to the nature of the pupa. Does it represent the last nymphal instar of an insect without metamorphosis, or is it a preliminary form of the adult? Long arguments have been presented on each side of the question, but it seems that a few pertinent facts will give a sufficient answer.

Naturally, since the pupa is formed inside the larva, when the larval cuticle is shed the pupa has the elongate form of the larva. On the other hand, the pupa has the imaginal compound eyes and the imaginal mouthparts, legs, and wings in a halfway stage of development. Clearly, therefore, the young pupa is a preliminary developmental stage of the imago modeled in the larval cuticle. Within the larval cuticle it undergoes a stage of development and reconstruction until when it finally casts off the larval skin it has the typical form of a pupa. Thereafter it does not change in external shape.

The body of the mature pupa takes on the form of the imago. Thus it serves as a mold for the newly forming adult muscles and allows them to become attached properly on the imaginal cuticle. This alone has been proposed as a theory adequate to explain the pupa as a preliminary adult stage. On the other hand, it has been held that this theory of the pupa involves the unusual occurrence of a moult in the stage of holometabolous insects. But the mayflies moult once after attaining a fully winged condition, and the apterygote insects, as well as most other arthropods, moult successively throughout life. Still the pupal moult may be regarded as a secondary one necessitated by the immaturity of the pupa. Moulting is determined by hormones, and hormones are powerful controlling agents in development. Insect endocrinologists have shown that they can make various adult insects moult again by transplanting into them the appropriate endocrine glands.

The larval skin containing the young pupa has often been called the “prepupal stage of the larva,” but with the moulting of the larval cuticle, not yet cast off, the larval life is ended. The young pupa ensheathed in the larval cuticle has been called the “prepupa,” but it is simply a young pupa in a formative stage and still cloaked in the larval skin. It is not distinct from the mature pupa which is ex-

posed at ecdysis when the larval skin is shed. The young pupa still enclosed in the larval cuticle has, therefore, been more properly named by Hinton (1958) the *pharate pupa* (from the Greek word for hidden or concealed). The same term would apply to any larval stage still cloaked in the skin of the preceding instar, and to the adult when it is still cloaked in the pupal skin. Among the muscoid flies, the larva completes its growth, changes to the pupa, and finally to the adult, all inside the cuticle of the third larval instar. The cuticle of the third larval instar becomes greatly modified during this time and it is termed the puparium after this modification; from the puparium the fully formed adult emerges.

Metamorphosis: The term is derived from the Greek words *meta*, a change, + *morphe*, form, + *osis*, a process of. Following its derivation the term metamorphosis means literally "a process of changing form," and it should be emphasized that the implied *change is one of form and not of substance*. Thus it is comparable to the change of water to ice, not to the replacement of ice crystals by salt crystals or something else. The term, however, is widely used in zoology for almost any conspicuous change of form that an animal makes during its development regardless of how this is done. The tadpole is said to metamorphose into a frog, but it does so by a continuous changing growth; and if this is metamorphosis then so is the embryonic development of any animal. The term probably originated with the early writers of fiction who were fond of inventing tales about human beings who, at the whim of some offended god or goddess, were transformed into other animals or trees. It is, of course, to be supposed that in such imaginary cases the flesh and bones of the human were directly transformed into those of the animal. The early naturalists took over the word metamorphosis and applied it to the seemingly similar transformations of insects such as that of a caterpillar into a butterfly at a time when it was perhaps not known that the caterpillar was simply a young butterfly. Once established, the word *metamorphosis* became a standard part of our entomological nomenclature well before the true nature of the change from larva to adult was known.

Modern studies on insect "metamorphosis" show that most of the larval tissues disintegrate and that the adult tissues and organs are newly built up in the pupa from cells that never formed an integral part of the larva. The adult cuticle is always a new secretion from the epidermal cells, which themselves may not change, though in some insects the larval epidermis itself is destroyed and replaced by an

adult epidermis formed from islands of imaginal cells in the larval epidermis. The alimentary canal goes into dissolution, and the adult food tract is generated from replacement cells in the wall of the larval canal. The larval musculature may be completely destroyed and new muscles for the adult formed in the pupa. Some organs such as the tracheal and nervous systems may be simply remodeled to serve the needs of the adult. How much reuse versus remodeling versus replacement is involved for the cells within the nervous system has not yet been determined, but it is clear that the nervous system is not replaced in toto as some other systems are. Clearly, most of this process of change is not a metamorphosis of larval tissues into adult tissues but a replacement of larval organs by newly formed adult organs. The result is an entire transformation in the *appearance* of the insect between larva and adult. This is because the two stages are really two different animals—one stage is not transformed into the other. The egg simply has the potentiality of forming first the larva and then the adult, as was clearly expressed by Janet long ago (1909).

The term *metamorphosis* has become so firmly established in entomological nomenclature that undoubtedly it will persist even if its erroneous implications become generally recognized. Insects have become famous for their metamorphoses.

If the young insect in the form of a larva does not grow into the adult of its species, it may be of interest to speculate on its nature and how it came to differ from its parents. We must suppose that primitively the young of all insects resembled their parents except in matters of immaturity, as do the young of a modern cockroach or grasshopper. With most of the higher insects, however, the winged adults have become specialized for a life and ways of feeding that the flightless young could not follow. The young left behind were forced to adopt ways of living suitable to themselves and so have undergone a juvenile evolution quite independent of their elders; they have become specialized for their own various habitats and ways of feeding. Thus the larval stages have acquired many diverse forms in the several orders and have become as distinctive of their species as their parents (this is shown by the fact that taxonomists have been able to construct keys to larvae as well as to adults, and in some groups it is easier to identify larvae than the adults). Insect larvae, therefore, are not ancestral forms though many of them have taken on a wormlike shape. Structurally they remain insects. It must be clear that the evolution of young insects into their specialized modern

larval forms is the *true metamorphosis* of the insects. When the larva has served its purpose in the life of its species, it is practically destroyed and the developmental process reverts to the adult, which alone can perpetuate the species. The larval destruction and the adult reconstruction take place simultaneously in the pupa which is itself a preliminary stage of the adult.

It is thus clear that the apparent change of the larval insect into the imago is not truly a metamorphosis. The term metamorphosis means literally "a change of form." The change from caterpillar to butterfly, however, is a change of form only in the eye of the beholder. Actually the change is a replacement of the larva by the butterfly. The writer has suggested the term *retromorphosis* for the reversion of morphogenesis to the adult line of development after the dissolution of the specialized larva (Snodgrass, 1961). The development of the adult and the destruction of the special larval tissues go on at the same time in the pupa, but the result is not a transformation of the larva into the adult.

Recapitulation: This term as applied to individual development implies that an animal in its ontogeny goes through stages of development that represent successive adult forms in its phylogenetic history. Garstang (1922) has severely criticized this theory in its general concept, contending that the ontogenetic form in one generation represents the ontogeny of preceding generations. This is particularly true of the larvae of holometabolous insects, which may be wholly adapted in their structure to their own way of living and feeding, and in no way represent adult ancestral forms of their species (see Larva, Metamorphosis).

The development of the insect embryo also is in many ways an adaptation to its life in an eggshell in which it cannot possibly follow the evolution of its free-living ancestors. In minor ways, however, the embryo is not necessarily prohibited from recapitulating the evolution of adult structures. It goes through a polypod stage, for example, when limb rudiments are present on all of the segments. At this stage it evidently represents a centipede-like ancestor. Moreover, the growth and development of all the appendages from simple undifferentiated lobes should repeat a similar origin of the limbs in some remote wormlike progenitor of the arthropods. Likewise, the development of wings from simple outgrowths of the integument, whether they remain on the surface or are temporarily sunken into pouches, would appear to repeat the evolutionary development of wings from paranotal lobes. In other words, ontogenetic recapitula-

tion may take place in organs that are not affected by the living conditions imposed on the embryo or the larva.

Moulting: The physiological process of separating the body cuticle from a new cuticle being formed beneath it by the epidermis. How this separation is accomplished is uncertain but it is soon made more obvious by the secretion from the epidermis of a moulting fluid which digests a greater or lesser amount of the old cuticle while the new cuticle is being secreted. The terms *moulting* and *ecdysis* have often been confused, with, as one result, the naming of the moulting hormone as "ecdysone." *Ecdysis*, *q.v.*, is literally the coming out of the insect from its moulted cuticle, and is not dependent on any hormone.

The phonetic spelling "molting" which recently has become current in the U. S. A. is not justified by the derivation of the word from the Latin *mutare*. The "u" is clearly the essential vowel, and it is retained in other languages, as *mudare* in Italian and *mudar* in Spanish and Portuguese.

Ecdysis: The word is derived from the Greek word meaning "coming out." It is properly pronounced ěk'-dĩ-sĩs but is commonly heard as ek-dy'-sis. The word has commonly been defined as synonymous with moulting, but the word can mean only the shedding or coming out of the moulted cuticle by the insect. Very commonly the newly moulted insect remains within the old cuticle for a variable length of time before emerging. With some insects, as the honey bee, the pupa goes through its preliminary change from the larval form within the last larval cuticle and comes out only when it has attained the final external form of the pupa. The most extreme case, however, is in the muscoid flies which form a puparium from the third larval cuticle, undergo the pupal stage within this, and then the adult emerges from it.

The insect within the moulted cuticle of the previous instar is the pharate (cloaked) period of the larva, pupa, or adult (Hinton, 1958).

Alimentary canal: The food tract of the mature insect always consists of three parts serially continuous but of different origins. The middle part, the *mesenteron*, represents the primitive endodermal stomach or archenteron of the gastrula; the anterior and posterior parts, the *stomodaeum* and *proctodaeum* respectively, are secondary ingrowths of the ectoderm. The origin and relations of the parts, however, are obscured in the development of the embryo by the various ways in which gastrulation takes place (see Gastrulation).

The two ends of the mesenteron must be interpreted as representing the two ends of the blastopore, though no distinct blastopore is formed in insect development. The anterior end of the mesenteron is, therefore, the primitive mouth, and the posterior end the primitive anus. With the ingrowth of the stomodaeum, however, the primary mouth is carried inward, and the anterior opening of the stomodaeum becomes secondarily the functional mouth of the adult. This mouth of the adult becomes surrounded during development by the outgrowing mouthparts and finally becomes enclosed by them in a space termed the *preoral food cavity* (often called the "mouth cavity" although, being outside the head, it is not truly a body cavity any more than is the space between the thoracic legs).

The stomodaeum has a strong muscular sheath consisting of an outer layer of circular fibers and an inner layer of longitudinal fibers. In the head there are also numerous dilator muscles from the head wall and from the tentorium. The stomodaeum is commonly differentiated into several parts. That just within the mouth may be called the *buccal cavity*, next is the *pharynx*, of different form in different groups, and then the tubular *oesophagus*. The oesophagus is usually enlarged posteriorly as a *crop*, though in some insects the crop is a diverticulum of the oesophagus. Following the crop is a short division, the *proventriculus*, which opens into the mesenteron through a funnel-like infolding of the stomach wall, known as the *stomodaeal valve*. The proventriculus is commonly armed internally with cuticular teeth or other structures that presumably give it the function of a gizzard to grind the food, but in other cases it may possibly serve as a strainer, or merely to regulate the passage of food into the stomach.

The mesenteron is usually a simple cylindrical sac, and it is the functional stomach or *ventriculus* of the insect. In some insects, however, it is divided into several parts (see Mesenteron). From the anterior end of the ventriculus there usually projects a circle of blind pouches, the *gastric caecae*, but tubular caecae may also be borne on other parts of the stomach in some species.

The proctodaeum is divided into two principal regions, an anterior tubular part, which may be termed the *anterior intestine*, and an enlarged posterior part commonly called the *rectum*. The end of the anterior intestine adjoining the stomach is termed the *pylorus* (gate keeper); it gives off the excretory *Malpighian tubules*. The part following the pylorus is often differentiated into an anterior *ileum* and a posterior *colon*. The rectum consists of a large anterior *rectal*

sac and a posterior narrow part or *rectum* proper. The terminal opening is the functional *anus*.

Gastrula: The Greek word *gaster* really means the paunch or belly, but as used in anatomy the *gaster* is the stomach. Gastrulation, therefore, should mean stomach-formation regardless of the method of formation.

Borradaile and Potts (Invertebrata, p. 127) state: "Every triploblastic animal passes through a stage—the *gastrula*—in which it consists only of ectoderm and endoderm. Save in this essential feature, the gastrulae of different animals may be extraordinarily unlike, and, especially when the animal is developed from a very yolky egg, they are sometimes very difficult to recognize as such; but where the gastrula is well formed, as in the familiar development of *Amphioxus* or in that of a starfish, its two-layered wall may always be found to contain a cavity, the *archenteron*, which possesses a single opening, the *blastopore*."

The first development of a metazoic egg commonly leads to a hollow mass of cells known as the *blastula*. If the *blastula* represents a free-living ancestral form it probably obtained its food from the water through its surface cells. If it commonly lived on the bottom it would be natural that the cells of the underside would become specialized for ingestion and digestion of food material. Then it would be a further advantage if this surface should sink into the *blastula*. Thus the animal would become a two-layered sac, the cavity of which would be the primitive stomach or *archenteron*, the opening of which is the *blastopore*. The outer cell layer becomes the *ectoderm*, the lining of the stomach becomes the *endoderm*.

In a few of the metazoic animals the stomach is formed during embryonic development by introversion of the ventral wall of the *blastula*. In an elongate animal the *blastopore* becomes divided into a mouth and an anus. This stage in the ancestors of the arthropods has been thought to be well represented in the onychophoran embryo which presents a median ventral groove that closes between the two ends. However, Manton (1949) finds that this groove is not the elongated *blastopore* because its formation does not give rise to the endoderm; the endoderm is proliferated internally from a generative area behind the groove. It is this generative area which thus represents the true *blastopore*. The mouth-anus groove, therefore, is a secondary formation, but evidently it must be formed in some way from the *blastopore*.

The method of endoderm formation by introversion is commonly

replaced by the internal proliferation of cells from the ventral surface of the blastoderm. It is bewildering to read the various conflicting accounts of gastrulation in the insects as reported by different writers and summarized by Johannsen and Butt (1941) and by DuPorte (1960), but much of the confusion results from not recognizing that introversion and proliferation may be just two superficially different ways of forming the endoderm.

Gastrulation: This is the process of formation of the stomach irrespective of the method by which it is accomplished. The word itself is derived from *gastrula*, the diminutive form of the Greek word *gaster*, which is used in anatomy for the functional stomach of an animal.

The first development of the egg commonly leads to the formation of a hollow mass of cells known as the *blastula*. If the blastula represents a free-living ancestral form of the Metazoa, it probably obtained its food from the water through its surface cells. If it commonly lived on the bottom of a body of water, the cells of the under-surface may be supposed to have become specialized for the ingestion and digestion of food material. It would then be an advantage if these cells should sink into the blastula forming a cavity in which the food could be carried about and more leisurely digested. This food cavity is the primitive stomach or *archenteron*, the opening of which is the blastopore. The outer cell layer of the body is the *ectoderm*, the wall of the stomach is the *endoderm*.

In the embryogeny of a few of the lower Metazoa the stomach is formed by this method of introversion of the digestive cells of the blastoderm. However, when the egg, as in most insects, contains a large amount of yolk which becomes surrounded by the blastoderm, gastrulation by introversion becomes entirely impractical. Aside from the mechanical difficulties of invagination when the center of the blastula is filled with yolk, introversion would place the yolk (food) in the body cavity and outside the stomach. The insect embryo, therefore, cannot recapitulate the primitive method of stomach formation; it must adopt some other method.

The ways by which the endoderm is formed by the insect embryo, as reviewed by Johannsen and Butt (1941) and by DuPorte (1960), are seemingly so various that it becomes bewildering to attempt to interpret them all as derived from introversion or some modification thereof. However, the process of infolding one wall of the blastula may be replaced by the immigration of single cells. Such cells are usually called *yolk cells*, but, since they presumably act as

vitellophags (yolk eaters), they probably serve for digestion of yolk during early stages of development; they should therefore be considered as endodermal. In some of the lower insects the yolk cells are said to form a stomach wall by investing the yolk. In such cases the yolk cells seem to demonstrate their endodermal nature.

With most of the higher insects a narrow ventral strip of the blastoderm becomes differentiated from the lateral plates, and either sinks into the yolk or is overgrown by the lateral plates. A ventral groove is thus formed along the ventral side of the blastoderm; this ventral groove has been regarded as a remnant of the elongated blastopore closed between the mouth anteriorly and the anus posteriorly. The enclosed ventral plate spreads out and divides into an inner endodermal layer and an outer mesodermal layer.

The early embryo of *Onychophora* presents a median ventral groove that eventually closes between the two ends which become the mouth and the anus. The onychophoran, therefore, has long been thought to give an example of the primitive blastopore of the arthropods. Manton (1949), however, has shown that this mouth-anus groove of the onychophoran is not the blastopore. The endoderm, she says, is proliferated from an area behind the anus, and cells from this area form the complete stomach epithelium. The mouth-anus groove is thus a secondary formation, though perhaps in some way derived from the blastopore.

Even in the insects it must be noted that the concavity of the ventral plate does not become the stomach lumen. The functional endoderm is proliferated from cell masses at the two ends of the endoderm, and in some cases also from the whole length of it. The growth of the definitive midgut epithelium from cell masses thus resembles the proliferation of endoderm in the *Onychophora* and of yolk cells in the lower insects. The business of endoderm is to surround the yolk in order to digest it. This is accomplished mostly by the anterior and posterior cell masses which send out ribbons or sheets of cells toward each other around the yolk; these eventually unite and form the stomach which thus comes to contain most or all of the remaining food (yolk) of the developing embryo.

Since in some cases the endoderm appears to be proliferated from the inner ends of the stomodaeum and proctodaeum, some embryologists have contended that the insect stomach is ectodermal. It is noted by Henson (1946), however, that the two ends of the stomach represent the extremities of the blastopore where naturally ectoderm should be generated externally and endoderm internally. It is evi-

dent, then, that while ancestral recapitulation plays no part in the formation of the insect's stomach, the embryo has adopted another method of gastrulation, namely cell proliferation, and thus does not violate the germ layer theory.

Mesenteron: As indicated by the origin of the word (Gr. *meso*, middle, + *enteron*, alimentary canal) this is the middle portion of the food tract. It extends from the ectodermal stomodaeum in front to the ectodermal proctodaeum behind, and it becomes the functional stomach of the insect, known as the *ventriculus*. It is probably always of endodermal origin though variously formed in the embryo (see Gastrulation; also Snodgrass, 1935, and DuPorte, 1960).

In form the mesenteron is typically an elongate cylindrical sac, but it may be a slender coiled tube, and in some insects it is differentiated by constrictions into several well-defined sections. The anterior part that surrounds the stomodaeal funnel is called the *cardia*. Blind tubular pouches, known as *gastric caecae* and varying in length and number, project from various parts of the stomach wall. Most commonly, however, they project from the anterior end of the stomach around the entrance of the stomodaeum.

The wall of the mesenteron is a thick epithelium of columnar cells separated from the hemocoel by a distinct basement membrane. Externally, beyond the basement membrane, there is a muscular sheath of longitudinally and circularly arranged fibers, but the arrangement differs from that around the stomodaeum and proctodaeum in that the longitudinal fibers are external to the circular ones. The inner ends of the epithelial cells are somewhat irregular and, as seen in sections, present what is known as a *striated border* due to the presence of alternating dark and clear lines that give a brushlike appearance. All the epithelial cells probably function for both secretion and absorption. Simple secretions are discharged through the striated border, but the cells also go through a disruptive process that has commonly been regarded as a form of holocrine secretion. Globules filled with granular material are extruded into the stomach lumen; these are then constricted and break off, followed by dissolution of their walls and the scattering of their contents. Whether this is a process of secretion discharge or simply a degeneration and dissolution of the cells, or both, it results in such a destruction of cells that they must be continuously replaced. Replacement is effected by groups of *regenerative cells* intercalated between the bases of the epithelial cells; by mitotic division these regenerative cells give rise to new cells that replace the worn out or discarded

ones of the epithelium. In some cases the regenerative cells are contained in crypts projecting on the outer surface of the stomach. In some insects the epithelium is completely regenerated at each moult, and the larval epithelium is always replaced by an adult epithelium at the last moult of holometabolous insects, usually forming for the imago an entirely new type of stomach adapted to the special food of the adult.

Usually there is one or more very thin sheets of secreted material separating the food from the surface of the midgut cells. This is the *peritrophic membrane*. In some cases (e.g., Diptera) it is clearly produced by a ring of cells at the anterior end of the mesenteron; in other cases (e.g., honey bee) it is delaminated from the surface of the mesenteron. The peritrophic membrane is composed of chitin and protein, and obviously must be sufficiently permeable to permit the ready passage through it of digestive enzymes and of digested products from the food.

Stomodaeum and proctodaeum: The primary mouth (Gr. *stoma*) of the arthropods represents the enclosed anterior end of the blastopore, but it is carried inward by the tubular ingrowth of the ectoderm known as the stomodaeum. Thereby the primary mouth becomes the opening of the stomodaeum into the stomach, and the functional mouth of the insect is the external opening of the stomodaeum.

Likewise, the primary anus (G. *proktos*) represents the open posterior end of the blastopore, but it is carried inward by an ingrowth of the ectoderm that forms the proctodaeum. Thereby the primary anus becomes the opening from the mesenteron into the proctodaeum, and the functional anus of the insect is the external opening of the proctodaeum.

The words stomodaeum and proctodaeum mean literally "on the way to the mouth" and "on the way to the anus," respectively. And this is just what they are! The *-daeum* part of these words is taken from the Greek *hodaïos* meaning "belonging to a way" (from *hodos*, a way or path). By eliding the *ho* and latinizing the rest of the word, *daeum* is obtained.

Head: The insect head is a continuously sclerotized cranium-like capsule. Its simpler or more generalized form and structure are best seen in the head of an insect such as a grasshopper or its relatives. In these the *face* is directed forward and the *mouthparts* hang downward. The *compound eyes* then have a lateral position, and the

antennae arise from the upper part of the face. The mouthparts (mandibles, maxillae, and labium) are suspended from the lower cranial margins, as the legs are from the thorax. The hypognathous head, therefore, should be primitive since the mouthparts represent appendages serially homologous with the legs. The ventral wall of the head is completely concealed by the mouthparts; it contains the mouth opening into the alimentary canal, and supports below the mouth a large median tonguelike organ known as the *hypopharynx*. The back of the head is perforated by a large opening into the neck; it is analogous to the foramen magnum of the vertebrate skull but is called the *occipital foramen* in insects.

The cranial areas are given specific names. The top of the head is the *vertex*; the facial area between the antennae and compound eyes is the *frons*; below the frons is an area known as the *clypeus*, from which is suspended the broad, free anterior lip called the *labrum*; the sides of the head are the *genae*; and the back is the *occiput*. These head areas are merely topographical regions, though some may be separated by grooves or *sulci* of the cranial wall. Most commonly present is a prominent *frontoclypeal* or *epistomal sulcus* separating the clypeus from the frons and forming a strong internal ridge between the mandibles. Even this sulcus and ridge, however, may be absent, as in the cockroach in which the frontoclypeal region is continuous. In some insects a vertical groove below each compound eye separates the gena from the frons. A groove near the lower edge of the gena may set off a narrow *subgenal* area; internally it forms a ridge that strengthens the genal margin for the support of the mandible and the maxilla. The subgenal sulcus is usually continuous anteriorly with the epistomal sulcus. The occiput may be separated from the vertex and genae by an *occipital sulcus*, but this sulcus is not commonly present.

The head includes at least four primitive body segments united with an anterior protocephalic part bearing the eyes and antennae. The four known head segments are a premandibular segment bearing in some insects a pair of vestigial appendages, a mandibular segment, a maxillary segment, and a second maxillary segment the appendages of which unite to form the labium. None of the head grooves mentioned in the preceding paragraph represent lines of segment union; they are merely cuticular inflections forming internal ridges for the strengthening of the head wall along lines of mechanical stress. On the back of the head, however, there is a groove of a different nature. It closely surrounds the occipital foramen dorsally and laterally, setting off a narrow *postocciput* be-

hind it and forming internally a deep ridge on which are attached muscles from the thorax that move the head. The fact that the basal angles of the labium are suspended from the postocciput indicates that the latter is a sclerotic remnant of the labial segment and that the *postoccipital sulcus* represents the intersegmental line between the first and second maxillary segments. This intersegmental line alone has been retained on the head to provide for muscle attachments from the thorax. Anterior to this line there are no somatic muscles in the head; there are only muscles connected with the appendages and with the proctodaeum. It is not to be concluded, however, that the narrow postoccipital flange of the head represents the entire labial segment; the segment may well include a part of the membranous neck too.

The mouth of the insect, as already mentioned, is in the concealed ventral wall of the head just above the base of the hypopharynx. Before the mouth, however, there is a large *preoral cavity* shut in by the mouthparts. Its anterior wall is the inner surface of the labrum and the clypeal region known as the *epipharynx*. Between the epipharynx and the base of the hypopharynx there is a food pocket, the *cibarium*, just before the mouth; the masticated food is deposited here before being taken into the mouth. The cibarium can be dilated by muscles from the clypeus, and contracted by transverse muscles in its anterior wall. In liquid-feeding insects, the cibarium becomes a sucking pump by the partial union of the edges of its epipharyngeal and hypopharyngeal walls. The duct of the thoracic salivary glands commonly opens into the preoral cavity above the base of the labium, but in some insects it enters the hypopharynx to open on it. In either case the saliva mixes with the food in the preoral cavity so that the food is all ready to be swallowed when taken into the mouth.

The cibarium was long regarded as the "pharynx" of the insect; hence we have the incongruous terms "epipharynx" and "hypopharynx" for parts outside the mouth and having no relation at all to the true *pharynx*, which is a part of the alimentary canal within the head. The misapplied terms are still in current usage because we have no appropriate substitutes for them. "Palatum" and "lingua" have been suggested, but both the palate and the tongue are properly intraoral.

The cranial walls are braced by an internal skeletal structure known as the *tentorium*. It consists essentially of two pairs of apodemal processes. A pair of posterior arms arises from pits at

the lower ends of the postoccipital sulcus; these grow transversely and unite into a posterior *tentorial bridge* just within the occipital foramen. A pair of anterior arms arises from the subgenal sulci above the mandibles, or more frequently in the epistomal sulcus; these grow posteriorly and unite with the posterior bridge. Primarily the tentorium therefore comes to have the shape of the Greek letter π , but often the space between the arms is partly filled by a central sclerotization giving the structure a resemblance to a canopy suspended by four stays. It is probable that the structure got its name from the latter situation because *tentorium* is the Latin word for "tent." In some of the apterygote insects the anterior arms are not yet united with the posterior bridge, and there is evidence that these arms were primitively ventral head apodemes. On the other hand, in some of the higher insects modifications take place resulting in either enlargement or reduction of the anterior arms, and in some cases an obliteration of the middle part of the bridge. Such modifications, however, are clearly secondary.

In immature insects the frontal region of the head is commonly marked by an inverted Y-shaped line the stem of which continues back over the vertex to the postoccipital margin. This line has long been called the "epicranial suture," and supposed to be an important structural feature of the head. It is now known, however, to be a preformed line of weakness in the cuticle where the head wall will split at ecdysis (Snodgrass, 1947). The line on the vertex is continuous with the splitting line on the back of the thorax, and the arms diverge downward on the face at various angles from the compound eyes to the clypeus. Only rarely is a remnant of this *ecdysial cleavage line* preserved on the head of an adult insect.

This account of an orthopteroid head will give the student a picture of the fundamental structure of the head in a pterygote insect. Numerous modifications, however, will be found in other orders according to the position the head takes on the neck and its adaptations to different feeding habits on the part of the insects. The orthopteran is said to be *hypognathous* because the mouthparts hang downward from the lower margins of the cranium. In a *prognathous* beetle with forwardly directed mouth parts, the change in position of the head on the neck has involved various alterations in the head structure, particularly in its lower parts. A third type of head is *opisthognathous*, as in the Hemiptera, in which the sucking beak projects backward beneath the thorax and so causes adaptive changes in the head structure. These and other derived types of head struc-

ture cannot be fully described here; the student must refer to special papers on the subject or to more general texts for wider information. In the study of any insect head, however, an attempt must always be made to homologize the special features encountered with the fundamental head structure from which the specialized types presumably have been derived. To correlate structural evolution with changes in function is the essence of morphology.

To understand fully the nature of the insect head it would be necessary to know its phylogenetic evolution. This we cannot know, but we can infer something about it from embryonic development. The primary embryonic head in all the arthropod groups is a large lobe at the anterior end of the body on which the eyes and antennae are developed, and which contains the primitive brain ganglia. This *protocephalon* or first head, therefore, is entirely a sensory region. The mouth is formed by ingrowth of the stomodaeum at the base of its under surface. If the protocephalon truly represents the primitive head of arthropods it might well be termed the *archicephalon*. But as the head of the embryo, without any phylogenetic implications, it has been well named the *blastocephalon* by DuPorte (*G. blastos*, a bud or sprout, generally in embryology for the first recognizable beginnings of something, as in blastoderm, blastopore, ectoblast, etc.).

Behind the protocephalon of the early embryo is a region of four body segments in front of the thorax. The first of these segments in some insects bears a pair of minute, transient limb vestiges which correspond to the second antennae of Crustacea, the second is the segment bearing the mandibles, the third is the segment of the first maxillae, and the fourth is that of the second maxillae which unite with each other in insects to form the labium. These four segments are eventually consolidated with the protocephalon to form the definitive head. The ganglia of the first of these segments are drawn forward and unite with the protocephalic brain to become the tritocerebral lobes of the definitive brain. The ganglia of the other three segments combine to become the suboesophageal ganglion of the mature head. These are the visible facts of the embryonic development of the head. Theories on head segmentation are not so simple.

Inasmuch as the embryonic head lobe lies in front of the mouth, bears the antennae and the eyes, and contains the primitive brain, it has been interpreted as representing the *prostomium* of the annelid worms (Holmgren and Hanstrom). This idea gives a very simple concept of the relation of the arthropods to the annelids. More recent embryological studies on the arthropods have, however, re-

vealed the presence of small, paired, temporary cavities in the mesoderm of the antennal region of the head, and another pair in the preantennal region. Some embryologists insist that any pair of coelomic sacs must represent a segment. They contend, therefore, that primitively the embryonic head lobe of insects contained both an antennal segment and a preantennal segment, thereby making six primary segments in the definitive head in addition to a small anterior prostomial region bearing the labrum. [The maximum number of segments in the insect head, based on these coelomic sacs, is nine according to Janet; four of these would be in front of the antennal segment, if the antenna does indeed represent a segment.] The contention is logical if we accept the premises. Coelomic sacs are spaces in the mesoderm for the accumulation of waste products of metabolism, and most of them have ducts leading to the exterior. The outer walls of the sacs form the longitudinal muscles that determine the segmentation of the ectoderm. Where there is no ectodermal segmentation, as in the embryonic head of modern arthropod embryos may we not question that coelomic sacs are always accompanied by ectodermal segments? Those of the embryonic head may have purely a physiological function (and a transitory one since they are not carried over to later stages of the insect). The reported presence of coelomic sacs in the labrum is particularly difficult to account for since few morphologists regard the labrum as representing a segment. The actuality of an antennal segment and a preantennal segment in the primitive head of insects may, therefore, be doubted, but not outright denied.

A theory of head segmentation promulgated a few years ago caused much confusion by its sensational claim that the tritocerebral lobes of the brain are the ganglia of a "labral segment," because the labral nerves are connected with them (Ferris). This idea was based on observation that the endings of body nerves remain in the segment of their origin even after their central ganglion has been transposed to another segment, and that thus one may identify the segment of the ganglion. This generalization is true for *motor nerves* which arise from the ganglia and grow outwardly to the part which they will innervate. The labral nerves in question, however, are *sensory nerves* arising in the labral epidermis and growing in to the tritocerebral ganglia. The origins of sensory nerves do not identify the segment of the ganglion to which the nerves go, and nothing indicates that the labrum is a head segment. We have here an excellent example of how revolutionary ideas can be drawn from logical reasoning based on false premises.

Epicranial suture: See Ecdysial Cleavage Line of Head.

Ecdysial cleavage line of head: This is the familiar inverted Y-shaped line on the front of the head of young insects. The stem of this line on the top of the head is continuous with the ecdysial line on the back of the thorax. The arms of the cleavage line ordinarily diverge downward on the face at various angles, but in some hymenopterous larvae the stem is unbranched and continues straight down the face to the labrum. Though the cleavage line on the head has long been known as the "epicranial suture," and regarded as an important structural feature of the cranium, it is in no sense a "suture." It is merely a preestablished line of weakness where the head cuticle will split at ecdysis. A remnant of the line is rarely retained as a groove on the adult head (Snodgrass, 1947).

Antenna: The antennae are paired segmented appendages of the head of the trilobites and most of the mandibulate arthropods. They are absent only in the Protura, the chelicerates, *Limulus*, the arachnids, and some insect larvae. In the diplopods, chilopods, symphylans, and the entognathous hexapods, the antennae consist of a variable number of divisions each of which is provided with muscles inserted on its base and arising in the proximal division. Such antennae, therefore, are fully segmented, and probably represent the primitive antennal structure. In the Thysanura and the pterygote insects, however, the antenna consists of a basal stalk or *scape*, a small intermediate *pedicel*, and a distal *flagellum* which is usually subdivided into a variable number of *annuli*. The only muscles in an antenna of this type arise on the scape and are inserted on the base of the pedicel. The flagellar annuli have no muscles and vary in number from one to many; evidently the flagellum is a single subdivided segment. The pedicel contains a large sensory organ known as the Organ of Johnson. If the pedicel is a separate segment then it must have lost its muscles. The thysanuran-apterygote antenna consists of not more than three segments.

Each antenna is movable as a whole by muscles arising in the head and inserted on its base. These muscles usually arise on the anterior arms of the tentorium. The whole antenna is set into a membranous socket of the head wall, and is pivoted on a point on the lower rim of this socket. Thereby it is freely movable in all directions.

The antennae serve as delicate organs of touch and are the principal seat of the olfactory sense of insects. In addition, some insects, such as the male mosquito, hear at least the tone of the female's wing vibrations by means of sensory hairs on the antennae.

Whether the antennae are segmental appendages serially homologous with the mouthparts and the thoracic legs is a question bound up with that of the segmentation of the head (*q. v.*). When an antenna is amputated, the flagellum may be regenerated in a form resembling the distal part of a leg, but the significance of this phenomenon is uncertain.

Neck: The neck of the insect is a cylindrical membranous connection between the head and the prothorax. It varies somewhat in length in different insects. There are usually various plates, called *cervical sclerites*, in its walls; a lateral pair of these may form a support for the head by articulating on the postoccipital margin of the latter. The flexible neck allows for movement of the head in various directions by muscles arising in the prothorax and inserting on the postocciput or the postoccipital ridge.

The morphology of the neck is difficult to understand from its musculature. The principal longitudinal muscles are dorsal muscles from the intersegmental phragma between the pronotum and the mesonotum and extending to the postoccipital ridge of the head, and ventral muscles from the prosternal apodemes to the cross bar of the tentorium. The extent of the muscles, therefore, might suggest that the neck is a part of the prothorax. In this case the postoccipital ridge of the head would be the intersegmental line between the labial segment and the prothorax, but this ridge is evidently the line between the maxillary and labial segments. Otherwise we have to assume that the muscles are those of two primary segments, the labial and the prothoracic, that have become continuous with the obliteration of the intersegmental fold between labial and prothoracic segments. The embryo gives no clue to this problem because the labial segment before it is added to the head is followed directly by the prothoracic segment. Unfortunately, the development of the neck musculature has not yet been followed in the embryo. A larva has no appreciable neck.

The number of head-neck muscles is variable in different insects. In the locust head, muscles arise from the pronotum as well as from the following phragma. When lateral neck plates are present they usually support the head on anterior processes, but when neck plates are absent the head may be supported on anterior processes of the prothoracic epineura. When a pair of lateral neck sclerites on each side are angularly articulated end to end, attached muscles, by reducing the angle, serve to protract the head. The variable structure of the neck contrasts with the standardized structure of a thoracic

segment, and suggests that the neck mechanism has been secondarily developed in the different insect orders.

Gula: The term is derived from the Latin word for gullet, windpipe, and neck, and in vertebrate anatomy it is used for the upper part of the ventral side of the neck next to the chin. In insect anatomy the gula refers to a ventral plate of the neck behind the base of the labium. It is commonly continuous with the postocciput of the cranium and may become united with the submentum of the labium behind the posterior tentorial pits. Since the anterior part of the neck is probably a membranous posterior part of the labial segment, both the postocciput and the gula appear to belong to the labial segment. The cervical sclerites lie behind the gula. A review of the literature is given by DuPorte (1962).

Thorax: The term is derived from the Greek word *thorax*, a breastplate of ancient Grecian armor; in anatomy it refers to the part of the human body covered by a breastplate. The thorax of insects is the locomotor section of the body between the head and the abdomen. It consists of three segments, the *prothorax*, *mesothorax*, and *metathorax*, as a result of the reduction of the number of walking legs to three pairs. Once established as the locomotor center, the thorax also became the site of wing development in the winged insects. Wings, however, are present only on the mesothorax and the metathorax, but either one of these pairs may be transformed into nonflight organs.

The thoracic wall of pterygote insects is necessarily well sclerotized and the presence of both legs and wings differentiates the circumference of the segments into tergal, pleural, and sternal. The tergal plates are termed *nota* (Greek) in order to combine properly with the Greek prefixes *pro-*, *meso-*, and *meta-*. The notum of the prothorax is relatively simple because of the absence of wings on this segment. In the winged segments, however, the notum becomes the essential lever for the wing movement since its lateral margins must vibrate up and down to give the vertical movement of the wings in flight. The notal movements result from an alternating longitudinal upward curvature and flattening of the notum produced by constriction of longitudinal and vertical muscles. In adaptation to its function, the wing-bearing notum must be properly flexible. It is typically divided by a V-shaped ridge-forming groove in the posterior part (the apex of the V is forward); this apparently controls the bending of the notum so that the principal lateral movements

occur at the bases of the wings. Anteriorly it is commonly marked by a transverse groove, and the resulting three areas of the notum are termed the *prescutum*, *scutum*, and *scutellum*. Close to the anterior margin is another transverse groove that forms a deep internal ridge, the *prephragma*, for the attachment of the longitudinal dorsal muscles. These muscles, however, are intersegmental, their posterior attachment being on the phragma of the following segment. The two segments, therefore, must be solidly attached, and this is accomplished by a lengthening of the precostal part of the following segment as a *postnotal plate* firmly joined to the scutellar margin of the preceding notum. The contracting muscles thus give a strong upward curvature to the wing-bearing notum which effects the depression of the wings in flight. Flattening of the notum results from the contraction of vertical notosternal muscles, and produces the upward movement of the wings.

In the 4-winged insects, the two winged segments are essentially alike, the postnotal plate of the second being derived from the first abdominal segment, and the third phragma likewise. In the clistogastrous Hymenoptera, the first abdominal segment is so thoroughly incorporated into the thorax during early pupal development that it becomes virtually a part of the thorax in the adult stage. The abdominal pedicel is then formed from the second abdominal segment.

The pleuron of a winged segment is marked by a deep vertical or inclined groove from the leg base to the wing base. This forms a strong internal *pleural ridge* to strengthen the pleural wall in its double duty of supporting both the leg and the wing (see Pleuron). The ridge forms the coxal articular process at its lower end, and the wing fulcrum at its upper end. In the prothorax, the ridge supports the leg but usually does not extend on to the back. The pleural ridge also usually gives off a strong apodemal arm directed inwardly. The pleural sulcus divides the pleural surface into an anterior *episternum* and a posterior *epimeron*, but these parts may themselves be further differentiated into areas by sulci or by desclerotization.

The sternal region of the thorax is generally continuously sclerotized in each segment except for small membranous areas between the major plates. The latter is often differentiated by a transverse groove into an anterior *basisternum* and a posterior *sternellum*. Between the two parts at the ends of the groove arises a pair of sternal apodemes which are commonly united at their bases to form a Y-shaped process known as the *furca*. The arms of the furca turn outward and are closely associated with the inner ends of the *pleural process*, the two being usually connected by short muscle fibers. The pleural

plates are then braced against the sternum. The small intersegmental sternites are known as the *spinasterna* because each usually supports a pair of internal processes for muscle attachments. There is, of course, much diversity in the relative size of the sternal parts in different insects, and a large part of the venter in each segment may be membranous. If the sternal sclerotization extends to the base of the leg on each side it forms a ventral articular process for the coxa.

While the above description applies to the thorax of most winged insects, there are structure and function variations in the different orders. In the honey bee, for example, a line of flexion in the mesonotum cuts across the posterior part of the scutum and scutellum between the bases of the wings. In two-winged insects the metathorax is generally much reduced in size but retains the fundamental thoracic structure, showing that the 4-winged condition is primitive for these groups.

Spiracle: The breathing apertures should be called spiracles from the Latin word *spiro*, to breathe, and *spiraculum*, a breathing hole. The term *stigmata* formerly given to them means "spots," and probably reflects the ignorance of the early entomologists regarding their function. A "stigma" was also a brand with which slaves were marked, and hence a blemish. The word should be discontinued as an entomological term.

A spiracle is more than simply a hole into a trachea; it is usually a depression of the cuticle into which the trachea opens, forming thus a spiracular atrium. Most spiracles have a special closing apparatus which may be the outer lips of the atrium but more commonly is a valvelike structure at the opening of the trachea operated by muscles.

Leg: The Latin word for leg is *crus*, *cruris*, but this word and its Greek equivalent *skelos* have not been adopted into anatomical terminology for the legs of an animal though we have the *crura cerebri* of the brain and *crural nerves* of the legs. On the other hand, the Latin *pes*, *pedis*, and the Greek *pous*, *podos*, each strictly meaning the foot, have become the basis of most leg names, as in biped, centipede, millipede, arthropod, diplopod, hexapod, etc.

In insect anatomy the word *leg* is used in a functional sense rather than a morphological one, since it is applied to the thoracic legs and to the abdominal prolegs of larvae though the two sets of organs have no homology. The thoracic legs represent the embryonic leg

rudiments which reach their full development as organs of locomotion only on the thorax. The appendages of the head became feeding organs; those of the abdomen are represented by vestiges in the embryo which disappear unless some of the external genital organs are derived from them.

The thoracic legs of the insects are 6-segmented; those of most other arthropods usually have seven segments. The segments, beginning at the leg base, are named *coxa*, *trochanter*, *femur*, *tibia*, *tarsus*, and *pretarsus*. In a 7-segmented arthropod leg there are two segments in the trochanteral region, the *basipodite* and the *ischiopodite*. A *leg segment* is best defined as a section of the limb independently movable by muscles. The tarsus may be a single segment, but it is commonly divided into as many as five small parts which, though they are frequently called "tarsal segments" are really sub-segments or *tarsomeres* since the only muscle of the tarsus are those of its base arising in the tibia. The pretarsus bears the terminal claws of the leg (often called tarsal claws). The pretarsus, however, is clearly an end segment of the leg corresponding with the crustacean dactylopodite. In some insects it is a simple clawlike segment; in others it becomes 3-clawed by the development of a pair of lateral claws, but generally the median claw is lost and the typical insect foot has only the pair of lateral claws.

The pretarsus has only a single ventral muscle of several branches arising in the more proximal segments of the leg; these attach on it by a long tendon traversing the tarsus. In this feature the insects resemble the centipedes (in the Crustacea there are both levators and depressors of the dactylopodite).

The *leg segments* are connected by short membranous areas that allow them movement on each other. These flexible areas are the true joints of the limbs (from the French word *joindre*, to join), and this term should not be used for the segments themselves. Movements of the segments are controlled by *articulations* between them which are sclerotic extensions through the joint membranes from the opposing ends of the segments. The movement of the distal segments at a joint depend on the nature of the articulation, some are dicondylic, others monocondylic.

The so-called *prolegs* of insect larvae are short, unsclerotized, cylindrical outgrowths of the body. They have no structural resemblance to the thoracic legs, and there is no proof that they originate from the abdominal leg vestiges usually present in the embryo. The best-known examples are those of the caterpillar, each of which end in a claw-bearing foot pad. Body muscles are attached

on the base of the proleg, but the principal muscle is a long bundle of fibers arising on the lateral wall of the body and attached distally in the foot pad. The prolegs of the caterpillar serve principally for the support of the long and heavy abdomen and for grasping a stem or twig when climbing.

Wings: Of all the animals that fly, the insects alone have wings developed independently as organs of flight. The others have converted a pair of legs into wings. To be sure, the winged creatures of fiction imitate the insects in having wings specially created for flight, but it is doubtful that any of them could really fly if alive.

The insect wings grow out in immature stages of the nonmetabolous orders as small flat lobes from the edges of the back on the mesothorax and metathorax. Some fossil insects have similar lobes on the prothorax, suggesting that the ancestors of the winged insects had three pairs of *paranotal lobes*. Since at this stage they could not have served for flight, it is postulated that at first the lobes enabled the insects to glide through the air a longer distance than they could jump (in the manner of flying squirrels, etc.). If the second and third lobes then became lengthened and flexible at their bases, they might have been able to flap up and down, and thus sustain the insect in the air longer.

From some such early stage of wing development it seems to have required some evolutionary experimenting to produce an efficient mechanism of flight. The dragonflies have the simplest way of moving the wings. Each wing is pivoted on a process of the pleuron and is moved by antagonistic muscles inserted on the wing base at opposite sides of the fulcrum. Yet the dragonflies even today are among the most efficient of flying insects. The cockroaches, mantids, and termites are weak flyers compared with the dragonflies, and it is not well understood just how they move their wings. They have neither the dragonfly mechanism nor the typical thoracic musculature of the higher insects. The wings in these groups are supported on pleural fulcra, and muscles acting on the wing base before and behind the fulcrum probably effect a depression of the wings, while it is possible that the numerous leg muscles attached on the back sufficiently flatten the notum to raise the wings. Though the thoracic musculature of these insects is well known, no real study has been made of its action on the wings.

The typical insect wing mechanism is found in the mayflies and in all the higher orders. It provides for the up-and-down wing movements and for a partial rotation of each wing on its long axis,

the latter being necessary for directed flight. Both sets of movements depend on a strong support of the wing on a pleural fulcrum.

The vertical wing movements result from an alternating upward curvature and flattening of the wing-bearing notum, the margins of which thus depress or elevate the attached wings on the fulcral supports. The notal movements are produced by the antagonistic contraction of the dorsal longitudinal muscles and the notosternal vertical muscles of the wing-bearing segments. But this action of the muscles involved some radical alterations in the thoracic structure. The dorsal muscles are intersegmental, and ordinarily serve to pull the two tergal plates together, accompanied by an infolding of the intersegmental membranes. To effect a dorsal curvature of the notum, therefore, the intersegmental membrane has to be replaced by a sclerotization that would solidly unite the consecutive notal plates. The sclerotized membrane forms the so-called *postnotum* of the back. The tension produced by the muscles must now effect an upward curvature of the notum, giving the downstroke of the wings. The upstroke then follows from the depression of the notum by the vertical notosternal muscles attached on it. With the development of the wings the dorsal muscles became enormously increased in size, and to accommodate them the notal ridges of their attachments have been expanded into large plates, the intersegmental *phragmata* of modern insects.

The wing being a flat fold of the body wall, its upper layer is continuous with the supporting notum, and its lower layer is reflected into the pleural wall. The basal region of the wing is largely membranous to allow for flexibility, but to maintain a hinge movement on the notum small sclerites are present in the membrane that articulate with specific wing processes of the notal margin. These sclerites, though on the upper surface of the wing, are known as the *axillaries*. A first axillary sclerite articulates with an anterior wing process of the notum, a third axillary with a posterior notal process. An intermediate second axillary loosely connects the other two and forms ventrally the pivotal point of the wing on the pleural wing fulcrum.

The mechanism that converts the flapping wing into an organ of flight pertains to the pleuron. The under surface of the wing is continued into the pleuron by wide membranous areas before and behind the pleural fulcrum. The wing, therefore, rocks freely on the fulcrum. In the membranes before and behind the latter are small sclerites, the *basalare* and *subalare* respectively, on each of which are attached vertical muscles. Since the sclerites are closely connected

with the wing base, contraction of the basalar muscles turns the wing somewhat forward and deflects its margin during the downstroke. With the upstroke, the subalar muscles turn the wing posteriorly and deflect its posterior margin. The wing thus acts as a propeller, and with the downstroke it exerts a backward pressure on the air that drives the insect forward.

This account of the flight mechanism must be understood to give only its fundamentals and the action of the muscles that is the basis of the wing action with most insects. Other factors, however, may complicate the picture, and variations in the thoracic structure in the different insect orders involve modifications in the wing and its mechanism. A notable example is the conversion of the hind wings of Diptera into small knobbed oscillating stalks called *halteres*, so called because they were first regarded as balancers. It has now been shown that they have a gyroscopic action in some way stabilizing the insect's flight. The development of the halteres leaves no doubt that they are the reduced metathoracic wings. Another example is the modification of the forewings of beetles into elytra which seem to be good protective shields but are of no help in flying.

For a fuller discussion of the principles of flight mechanics and aerodynamics than can be given here the student is referred to the book "Insect Flight" by Pringle (1957).

Returning to the anatomy of the wings, the primitive wing lobes have been lengthened and properly shaped during their evolution into organs of flight. Necessarily, the wings must be as thin and light as possible, and at the same time stiff enough to withstand air pressure. This involved the development of lines of rigid, branching thickenings known as the *wing veins*. An old idea is that the veins were formed around tracheae, but this is not supported by recent critical studies (see Whitten, 1962). Another old idea is that the wings were first gills, but this idea has been superseded by the glider theory of wing origin. The venational pattern must have been established early in the evolution of wings since the wing veins seem to conform to a fundamental pattern which permits a generally uniform nomenclature.

In the holometabolous insects the *wing buds* of the embryo are sunken into pockets of the epidermis. These pockets become closed off externally, and remain thus concealed throughout larval life. The larva is thus not encumbered with externally growing wings, and none of the thoracic modifications related to the wings are developed until the pupal stage. Throughout the whole span of its life, then,

the larva preserves the larval simplicity of its thoracic segments. The wing rudiments continue to grow in their pockets, and at the moult to the pupa they become evaginated as well developed lobes resembling the wing pads of hemimetabolous nymphs. Their final development, together with that of the adult thoracic structure is then developed within the pupa, so that the emerging adult is fully able to fly. In most cases the adult has to expand the wings and allow them to dry and harden, but in some aquatic groups (e.g., mayflies) the adults emerge and fly immediately.

It is clear that the evolution of the wings and of the thoracic modifications that enabled the glider lobes of the early insects to become organs of flight must have been a long and complex process. The winged insects, however, owe almost all that they are today to their wings. Note what simple creatures by comparison are the apterygotes, which probably have changed little since the time they first became hexapods. The wings of higher insects freed the adults from a ground existence, and many of them have taken advantage of their freedom to adopt new kinds of food and new ways of feeding, for which they have developed new types of mouthparts. The young in such cases could not lead the lives of their parents, and have become adapted to habitats and ways of living of their own. Thus it has come about that the young of these insects have been specialized to such an extent that they have lost all resemblance to their parents. The adult development is then delayed to the end of the larval life when the special larval tissues are destroyed in the pupa. This change from larva to adult is commonly known as metamorphosis, but really it is largely a replacement of the larva by the adult.

Abdomen: The name "abdomen" for the third section of the insect body does not clearly follow from its derivation; however, the insect abdomen does contain the principal viscera, and thus it may be likened to the vertebrate abdomen.

The primitive abdomen probably had 12 segments, this number being present in some embryos and in adults of the Protura. The terminal segment bearing the anus is probably a telson, since the last embryonic appendages in the embryo, which are retained as the cerci, pertain to the penultimate or eleventh segment. In most adult insects, however, there are only 10 abdominal segments, and the cerci are carried by the tenth segment and the anus is contained in an apical lobe.

The base of the abdomen may be broadly joined to the thorax or narrowed to a petiole. In the Hymenoptera the first abdominal seg-

ment is incorporated into the thorax as the propodium, and the second segment forms a petiole. The petiolate part of the abdomen is sometimes called the "gaster," but this is an inappropriate name for it, since the gaster is properly the stomach.

Male genitalia: The external genital equipment of male insects includes primarily organs for the insemination of the female and secondarily copulatory organs for holding her. To the taxonomist the male genitalia offer the best characters he has for the separation of species because of their highly diversified structure. This very fact, however, makes the study of the genital homologies difficult and has given rise to a great deal of confusion in current terminology. Recent studies on the development of the organs have given a better understanding of their basic structure and the homologies of the parts. Thus there has been made possible the adoption of a more uniform nomenclature. That confusion still persists is due largely to the fact that specialists in each order of insects insist on retaining their traditional ordinal nomenclature.

Since the inner organs of reproduction are duplicated on opposite sides of the body, and each has its own outlet duct, it is probable that primitively the ducts opened through paired external apertures, as they still do in some arthropods other than the insects. For efficient insemination of the female it became more practical to have the openings of the male ducts carried out to the ends of simple tubular outgrowths. Thus we find paired *penes* present in Crustacea and Diplopoda and, among the insects, in Ephemeroidea and Dermaptera. In most of the crustaceans and diplopods the penes arise on the bases of a pair of legs and are not themselves intromittent in function. The sperm is transferred from the male to the receptacle of the female by one or two pairs of modified legs (gonopods) of a following body segment. The insects have not adopted this indirect method of insemination, but they have developed a great variety of structures in the copulatory organs, associated with the organ of insemination, for grasping and holding the female.

The penes of Ephemeroptera arise from a small ventral plate or a pair of plates above the stylus-bearing plates of the ninth segment; these evidently belong to the much reduced tenth segment of the abdomen. The penes vary in form in different species, in some that are armed with subterminal prongs, and rarely they are united basally in a single organ, but the ducts are always separate.

In the Dermaptera the two penes are united basally on a long apodemal plate and are variously developed in their distal parts, so

that they have little resemblance to the simple organs of the Ephemeroptera. Distally each organ splits into a median tube containing the exit duct and a strong outer lobe. In some species the two penes are united in a single organ with three terminal lobes, the median one giving exit to the two ducts, or to only a single duct if one duct is reduced and nonfunctional. The Dermaptera thus give an example of the modification potential of paired penes.

The division of each *penis* in the Dermaptera into a mesal lobe containing the duct and into a clasperlike lateral lobe is suggestive of the division of each primary phallic lobe of the higher insects into a mesomere and a paramere. In the latter, however, the ducts never enter the mesomeres but unite with a common duct formed between their bases.

The Thysanura in the adult stage have a single median penis arising between the bases of the ninth segment stylus-bearing plates; into the base of this the two genital ducts open by a common orifice. The penis, however, is developed from two small primary lobes that become concave on their opposed surfaces and unite to form the tubular organ of the adult. The penis lobes have no connection with the stylus-bearing plates of the ninth segment, and thus would appear to belong to the tenth segment. Heymons (1899) has noted that in fact the embryonic ducts of *Lepisma* end in the tenth abdominal segment.

In the Orthoptera and the higher insect orders, a new type of genital apparatus appears. It likewise begins as a pair of simple lobes, but the lobes do not give exit to the genital ducts. The paired ducts open into a single duct that grows inward between the lobes and becomes the unpaired ejaculatory duct of the adult. It is perhaps possible that the two lobes in this case are the paired penes of the lower insects from which the ducts have withdrawn, but there is no direct evidence for such. A common idea has been that the primary genital lobes are rudiments of appendages serially homologous with the embryonic limb vestiges of the pregenital abdominal segments and the thoracic legs. They arise, however, close together on the venter of the ninth segment in nymphal or late larval stages after the disappearance of the embryonic limb vestiges. Their position on the ninth segment is always behind the area of the sternal plate. Possibly, therefore, they belong to the tenth segment as do the penes of the lower insects, and have been moved forward into the "inter-segmental" membrane of the ninth segment. In any case, the future history of these primary genital lobes has no counterpart in the lower insects.

Each primary lobe divides distally into two secondary lobes, a median *mesomere*, and a lateral *paramere*. Then in most cases the mesomeres unite by their edges to form a hollow median organ, the *aedeagus*, with the gonopore in its base; the lateral parameres become the claspers of the adult. The genital organs of the Orthoptera begin their development in this way as a pair of lobes that divide, but in their later growth they take on such a diversity of structure in the different families that the adult organs have little or no likeness to the genitalia of the other orders.

It is in the Hemiptera that we first encounter the genitalic structure typical of the higher orders. The mesomeres of the primary genital rudiments unite to form the median aedeagus, the parameres become the adult genital claspers. This same genitalic complex, though with many modifications, can be followed through to the most highly evolved orders. The parameres may be simple lobes, as in Hemiptera and Coleoptera, but in the other orders each is usually differentiated into a basal part and a muscularly movable distal part.

The known development of the genitalia leaves little doubt of the homologies of the major parts in the different orders. A great diversity in the genitalic nomenclature from one order to another, however, has grown up because most taxonomists are ordinal specialists and hence are interested in maintaining an established set of descriptive names handed down from their predecessors. This contrasts with their proclivity at changing the Latin names of the species and genera with which they deal. But a uniform nomenclature is desirable, as well as now being possible, and the lack of a uniform genital terminology is highly inconvenient to the nonspecialist and must be distressing to teachers and their students.

The common assumption that the primary genital lobes represent a pair of former legs has given the parameres the theoretical status of "gonopods." When divided, the basal part is identified as the "gonocoxite," the distal part as the "gonostylus." The aedeagus is then supposed to have been formed by the union of endite lobes of the "coxites." All this does very well as a basis for a practical nomenclature, but a leg origin of the genitalia has never been demonstrated or even supported by any concrete evidence. The postembryonic origin of the primary lobes and their median position behind the sternum of the ninth abdominal segment are in strong contrast to the true limb vestiges seen in the embryonic abdomen. There is no evidence that the mesomeres are endite lobes of the parameres. The primary genital lobes arise on the venter of the ninth abdominal segment, but always behind the region of the sternal plate. The adult

organ, aedeagus and parameres, therefore, is supported on the posterior margin of the ninth sternum. When the parameres are separated from the aedeagus, they appear to be independent appendages of the ninth sternum, and have been regarded as such. The fact, however, that the parameres always originate as lateral branches of the genital rudiments shows that their lateral position results from a secondary displacement giving them a mechanical advantage as independently movable clasping organs. The subsequent division of the parameres into "coxites" and "styli" occurs secondarily and only in the higher orders. It seems desirable, therefore, to adopt a nomenclature free from unproven hypothetical assumptions of dubious validity.

The genital claspers need no other name than that of parameres (side parts), a name first given to them in the Coleoptera. The two segments have been called the "basimere" and the "telomere," which terms to be specific should be *basiparamere* and *teloparamere*. When the distal segments resemble grappling hooks they have appropriately been called *harpagones* (sing. *harpago*). The median organ that gives exit to the ejaculatory duct is best termed the aedeagus (*q. v.*) because the word means simply the principal genital part. By the dipterists it has been called the *mesosome*, by others the *phallus* or *phallosome*, or more generally the penis. Since the functional intromittent organ is usually the everted membranous inner wall of the aedeagus with the gonopore at its tip, this structure is more literally a penis.

The name phallus is not inappropriate for the medium genital organ alone, but the latter has for so long been known to entomologists as the aedeagus that this term has entomological priority, and the insect organ has no homologue even in other arthropods. The word "phallus" in ancient Greek was a vertebrate term and was specifically applied to an artifact, symbolical of generation, carried in certain processions.

Since we seem to lack a good general name for the genitalia of the insects, the writer (1941) has suggested that the term *phallus* might, consistent with its original meaning, be applied to the entire genital structure developed from the primary rudiments. The word combines euphoniously with prefixes and suffixes. The aedeagus and parameres are often not separated at their bases, in which case the three parts form a phallic unit with a common *phallobase*. The eversible inner tube of the aedeagus which serves as the functional penis of the insect may then be termed the *endophallus* (more

euphonious than "endoaedeagus") in distinction to the outer genital parts as ectophallic structures. The primary genital lobes thus become the *phallic rudiments* and their branches *phallomeres*. The distal aperture of the aedeagus is the *phallotreme*.

This suggested nomenclature applies to only the major parts of the male genitalia which can be consistently named on a basis of homology. In all the insect orders, however, there are numerous secondary developments, and these structures must be given special names by workers in each order.

Aedeagus (variously written also aedaeagus, aedegus, aedoeagus, oedagus, edoegus, from Greek pl. *oidoia*, the genitalia + *agos*, chief or leader): The median organ of the male genitalia characteristic of pterygote insects from Hemiptera to Hymenoptera. The ejaculatory duct opens into it. The aedeagus is thus, as the name implies, the principal member of the genital complex. It is formed by the union of the two mesal branches (mesomeres) of the primary genital lobes at the sides of the gonopore. The gonopore, therefore, opens into the base of the aedeagal lumen, which latter is thus a secondarily added part of the genital exit passage, not a continuation of the ejaculatory duct, and its distal opening, the *phallotreme*, is not the gonopore.

The aedeagus is commonly known as the *penis* of the insect, but usually the whole organ does not serve for sperm intromission. The spermatazoa are discharged from the duct into the lumen of the aedeagus and then introduced into the female by eversion of the membranous inner wall of the aedeagus as a vesicle, or a long slender tube with the gonopore at its tip. This eversible tube, or *endophallus*, thus becomes the functional penis. In some insects the spermatozoa are encapsulated in a spermatophore, which during coition is attached to the opening of the spermathecal duct of the female. With others they are freely discharged either into the genital chamber of the female, from which they may make their way into the spermatheca, or they are introduced directly into the sperm receptacle. The endophallus may become a highly developed complex organ in itself, as in the honey bee, in which the outer part of the aedeagus is reduced to a pair of small plates guarding the phallotreme.

Though the aedeagus is fundamentally a tubular organ, it takes on various forms in different orders and families. In some Hymenoptera the lateral parts of the aedeagus become separated as a pair of free prongs (*sagittae*) from a median penis tube. Among the Diptera long rodlike processes (*paraphyses*) grow out from the aedeagal base.

When the aedeagus and the parameres are not separated at their bases, the three parts arise from a common *phallobase*, as among Coleoptera. In some cases the base of the aedeagus is connected with the parameres by a pair of small basal plates, or again the parameres may be entirely separated from the aedeagus.

Among the dipterists the aedeagus is known as the "mesosome," but this term (middle body) is not in itself specific for a genital organ. Others use the name *phallus*, which is from the Greek word for the male vertebrate organ with which the insect aedeagus has no possible homology (and in its ancient usage the "phallus" was particularly an artificial symbol of generation). *Aedeagus* is specifically an entomological term since the organ has no homologue even in other arthropods. Under the dissertation on Male Genitalia (*q. v.*) the writer has proposed that the term *phallus* is a convenient name for the whole genital complex developed from the primary genital rudiments.

Ovipositor: According to its derivation the word ovipositor should be applicable to any organ used for placing eggs. Among the insects, then, there are two types of ovipositors, one being the extensible abdomen itself, the other special pronglike outgrowths of the abdomen.

An ovipositor of the first type is present in the tubuliferous Thysanoptera, the Mecoptera, the Lepidoptera, the Coleoptera, and the Diptera. In these insects the distal part of the abdomen can be extended as a tapering, telescopic tube, near the end of which is the opening of the oviduct. Some of these insects deposit their eggs on exposed surfaces and protect them with a covering of glandular secretion. Others use the extended abdomen for inserting the eggs under the edges of loose bark, or into crevices, or for depositing them in rafts on the surface of water. In some of the fruit flies the greatly elongated abdomen has a sharp terminal point that enables the female to pierce the skin of fruit and insert their eggs into the flesh. A similar piercing tip is found in some primitive moths.

An ovipositor of the second type composed of movable sclerotic prongs is the organ usually referred to as the insect ovipositor. It is present in a very simple form in the Thysanura but is developed as a complex organ in some Odonata, in the Orthoptera, in the Hemiptera, and in the Hymenoptera. In these insects the ovipositor consists of two or three pairs of closely associated processes supported on two pairs of ventrolateral plates of the eighth and ninth abdominal segments.

An outgrowing genital process is in general a *gonapophysis*, a term applicable to the male as well as to the female. Specifically the prongs of the ovipositor are called the *valvulae* and the supporting plates the *valvifers* (valve carriers). The word *valva* in Latin was the name for one of a pair of folding doors; in modern mechanics a valve is a device for shutting off the flow of gas or water through a pipe, and in anatomy a valve is a fold in a blood vessel or the heart wall that regulates the flow of blood. Clearly, then, the use of the term *valves*, or the diminutive *valvulae*, for the prongs of the insect ovipositor has no justification from the original meaning of the word. The ovipositor is not a closing apparatus but a conducting organ. However, since we cannot well describe objects or anatomical parts without having names for them, the terms *valvulae* and *valvifers* will be used in the following description for the lack of appropriate substitutes.

In the typical pterygote ovipositor the free part of the organ is usually a tapering shaft composed of the first and second *valvulae* which enclose a narrow passageway for the eggs discharged from the opening of the oviduct between their bases. The ventral first *valvulae* slide back and forth on the second *valvulae* by interlocking ridges and grooves, and the second *valvulae* have a similar movement of their own alternating with that of the first *valvulae*. The movements of the *valvulae* are produced by muscles of the supporting *valvifers*, since the *valvulae* arise from the anterior ventral angles of their respective *valvifers*. The second *valvifers* are rocked on the lower edges, or sometimes on pivots, of the ninth tergum by strong antagonistic anterior and posterior muscles arising dorsally on the tergum. This imparts a back-and-forth movement to the second *valvulae*, which often united, giving a stronger support for the first *valvulae*. The first *valvifers* are small plates articulated on the anterior ends of the second *valvifers*, and each is provided with a muscle from the eighth tergum. The up-and-down movements of the first *valvifers* give a back-and-forth movement to the first *valvulae* on the second *valvulae*. The movements of the *valvulae* on each other carry the eggs through the channel of the ovipositor. The so-called third *valvulae*, when present, are usually either slender styluslike processes projecting from the rear ends of the second *valvifers*, or flat lobes that ensheath the distal end of the ovipositor shaft, but in some Orthoptera they are broad lateral plates of the shaft.

There are, of course, many variations in the size and shape of the ovipositor in the several orders of pterygote insects, but the general structure and mechanism of the organ are essentially the same

in all. Insects that possess this type of ovipositor are able to deposit their eggs in the ground, to insert them into the stems and twigs of trees, or into the bodies of other insects. The ovipositor of some Odonata is a well-developed piercing organ by which the female inserts her eggs into the stems of underwater plants. In other Odonata the ovipositor has become greatly reduced and nonfunctional; such species merely drop their eggs on the water during flight. In the wasps and the bees the ovipositor has been remodeled into a stinging organ for the injection of poison from glands opening into its base. The eggs of these insects are discharged directly from the opening of the oviduct at the base of the sting.

Theoretically the ovipositor has been interpreted as a development from primitive legs of the eighth and ninth abdominal segments. The valvifers are supposed to be the coxae, the first and second valvulae to be coxal outgrowths, or gonapophyses, and the third valvulae perhaps coxal styli of the second valvifers. Superficially this interpretation looks plausible since the valvifers are moved by muscles arising on the terga of their respective segments, and a comparison with the simple ovipositor of *Thysanura* at first sight appears to bear out the suggested homologies. The two long slender gonapophyses of each genital segment of the *Thysanura* appear to arise from the anterior mesal angles of the stylus-bearing coxal plates. However, they are only closely attached to these plates, and their basal muscles arise on the sternal area or a sternal plate between them. The gonapophyses have no musculature from the coxal plates, as they should have if they are either telopodites of the limbs or gonapophyses of the coxae.

Matsuda (1957, 1958) has given a critical historical review of work on the structure of the insect ovipositor and of opinions that have been held on the homologies of its parts. Among the earlier writers, Heymons (1899 and earlier papers) was the foremost proponent of the concept that the gonapophyses (prongs of the ovipositor) are secondary ectodermal outgrowths of the eighth and ninth abdominal sterna in no way related to the transient embryonic limb vestiges on the other segments of pterygote insects, or to the stylus-bearing coxal plates of *Thysanura*. Tillyard (1917) notes that in the Odonata the rudiments of the ovipositor develop early in the larval life, "but have nothing to do with the primitive paired segmental appendages of the abdomen, which are lost during embryonic life." On the contrary, most subsequent writers down to the present time have held to the theory that the ovipositor represents a pair of abdominal limbs of which the valvifers are the coxae. From a com-

parative study of the ovipositor muscles, however, Matsuda concludes that the musculature does not support the idea that the ovipositor has been derived from a pair of abdominal limbs. He concludes that the valvifers are sternal in origin, as claimed by Heymons. Certainly the ontogenetic origin of the ovipositor in the larva does not suggest that its rudiments represent legs. In the higher insects, as the writer (1933) has shown in the honey bee, the ovipositor is developed from two slender median processes on the venter of the eighth abdominal segment and two pairs on the ninth. These processes no more suggest a homology with legs than do the rudiments of the male genitalia.

Hence, if we do not wish to discard the idea of the leg origin of the ovipositor, the subject must remain doubtful until substantiated by better evidence than is at present available. The ovipositor is an organ peculiar to the insects that possess it. In no other arthropod is there any such structure, either anatomical or functional, associated with the opening of the oviduct.

Morphological generalizations are mental products of morphologists, but they are always intriguing in that they bring a lot of seemingly unrelated facts into a single concept. In this way they may be more convincing by the mental peace and satisfaction they give than by the evidence from the facts on which they are based. We must be cautious, then, not to accept a generalization on its mental appeal alone.

LITERATURE CITED

BORRADAILE, L. A., and POTTS, F. A.

1958. *The Invertebrata*, ed. 3 (edited by G. A. Kerkut), 795 pp. Cambridge University Press.

DUPORTE, E. M.

1960. Gastrulation and the endoderm problem in insects. *Ann. Ent. Soc. Quebec*, vol. 6, pp. 45-52.

1962. Origin of the gula insects. *Can. Journ. Zool.*, vol. 40, pp. 381-384.

GARSTANG, W.

1922. The theory of recapitulation: A critical restatement of the biogenetic law. *Journ. Linn. Soc. London, Zool.*, vol. 35, pp. 81-101.

HENSON, H.

1946. The theoretical aspect of insect metamorphosis. *Biol. Rev.*, vol. 21, pp. 1-14.

HEYMONS, R.

1899. *Der morphologische Bau der Insektenabdomens. Eine kritische Zusammenstellung der wesentlichen Forschungsergebnisse auf anatomischen und embryologischen Gebiete.* *Zool. Centralb.*, vol. 6, pp. 537-556.

HINTON, H. E.

1947. The insect cranium and the "epicranial suture." *Smithsonian Misc. Coll.*, vol. 107, No. 7, 52 pp.

1958. Concealed phases in the metamorphosis of insects. *Sci. Progress*, No. 182, pp. 260-275.

JANET, C.

1909. *Sur l'ontogénèse de l'insecte*, 129 pp. Limoges.

JOHANNSEN, O. A., and BUTT, F. H.

1941. *The embryology of insects and myriapods*, 462 pp. McGraw-Hill Book Co., New York.

MANTON, S. M.

1949. Studies on the Onychophora, VII: The early embryonic stages of *Peripatopsis*. *Philos. Trans. Roy. Soc. London*, ser. B, vol. 233, pp. 483-580.

MATSUDA, R.

1957. Comparative morphology of the abdomen of a machilid and a raphidiid. *Trans. Amer. Ent. Soc.*, vol. 83, pp. 39-63.

1958. On the origin of the external genitalia of insects. *Ann. Ent. Soc. America*, vol. 51, pp. 84-94.

PRINGLE, J. W. S.

1957. *Insect flight*. Cambridge University Press.

SNODGRASS, R. E.

1933. Morphology of the insect abdomen, II: The genital ducts and the ovipositor. *Smithsonian Misc. Coll.*, vol. 89, No. 8, 148 pp.

1935. The history of an insect's abdomen. *Ann. Rep. Smithsonian Inst. for 1933*, pp. 263-287.

1936. Morphology of the insect abdomen, III: The male genitalia. *Smithsonian Misc. Coll.*, vol. 95, No. 14, 96 pp.

1941. The male genitalia of Hymenoptera. *Smithsonian Misc. Coll.*, vol. 99, No. 14, 119 pp.

1954. Insect metamorphosis. *Smithsonian Misc. Coll.*, vol. 122, No. 9, 124 pp.

1960. Facts and theories concerning the insect head. *Smithsonian Misc. Coll.*, vol. 142, No. 1, 61 pp.

1961. Insect metamorphosis and retromorphosis. *Trans. Amer. Ent. Soc.*, vol. 87, pp. 273-280.

TILLYARD, R. J.

1917. *The biology of dragonflies*, 396 pp. Cambridge University Press.

WHITTEN, J. M.

1962. Homology and development of insect wing tracheae. *Ann. Ent. Soc. America*, vol. 55, pp. 288-295.

INDEX

- Abdomen, 36
- Aedeagus, 39, 40, 41, 42
- Alimentary canal, 15
- Anapleurite, 7
- Anatomical names, 1
- Annulus (annuli), 3, 27
- Antecostae, 3
- Antenna (antennae), 22, 27
- Anus, 21
- Archenteron, 17, 18
- Archicephalon, 25
- Articulations, 32
- Axillaries, 34

- Basalare, 8, 34
- Basiparamere, 40
- Basipodite, 32
- Basisternum, 30
- Blastocephalon, 25
- Blastopore, 16, 17, 19
- Blastula, 18
- Body segmentation, 2
- Buccal cavity, 16

- Caecae, 16, 20
- Cardia, 20
- Catapleurite, 7
- Cervical sclerites, 28
- Chorion, 2
- Cibarium, 2, 23
- Clypeus, 22
- Coelomic sacs, 3, 26
- Colon, 16
- Coxa (coxae), 7, 8, 32, 44
- Coxites, 39, 40
- Coxopodite, 9
- Crop, 16

- Dorsum, 4, 6

- Ecdysial cleavage line of head, 24, 27
- Ecdysis, 15, 24
- Ectoderm, 17, 18
- Embryo, 25
- Endoderm, 17, 18
- Endophallus, 40, 41

- Entomology, 1
- Epicranial suture, 24, 27
- Epimeron, 4, 8, 30
- Epipharynx, 2, 23
- Episternum, 4, 8, 30
- Epistomal sulcus, 22
- Eyes, compound, 21

- Face, 21
- Femur, 32
- Flagellum, 4, 27
- Frons, 22
- Frontoclypeal sulcus, 22
- Furca, 30

- Gaster, 37
- Gastric caecae, 16, 20
- Gastrula, 17, 18
- Gastrulation, 18
- Genae, 22
- Genitalia, male, 37
- Gonocoxite, 9, 39
- Gonopods, 37, 39
- Gonopophyses, 43, 44
- Gonopore, 41
- Gonostylus, 39
- Grooves, external, 8
- Gula, 29

- Halteres, 35
- Harpago (harpagones), 40
- Head, 21
- Hexapoda, 1
- Hypognathous head, 22, 24
- Hypopharynx, 2, 22, 23

- Ileum, 16
- Imago, 11
- Insect, 1
- Intestine, anterior, 16
- Ischiopodite, 32

- Labium (labia), 22, 29
- Labrum (labra), 22
- Larva (larvae), 9, 10, 11, 13, 14

- Legs, 8, 31
- Leg segments, 32

- Male genitalia, 37
- Malpighian tubules, 16
- Mandibles, 22
- Maxilla (maxillae), 22
- Mesenteron, 15, 16, 20
- Mesomere, 39
- Mesosome, 40
- Mesothorax, 29
- Metamorphosis, 10, 12, 13, 14, 36
- Metathorax, 29
- Moulting, 15
- Mouthparts, 16, 21, 22, 23, 24
- Muscles, 3, 28, 30, 32, 33, 34

- Neck, 28
- Nerves, 26
- Notum (nota), 4, 6, 7, 29
- Nymph, 9

- Occipital foramen, 22
- Occipital sulcus, 22
- Occiput, 22
- Oesophagus, 16
- Opisthognathous head, 24
- Organ of Johnson, 27
- Ovipositor, 42

- Paramere, 39, 42
- Paranotal lobes, 4, 33
- Paraphyses, 41
- Pedicel, 27
- Penis (penes), 37, 38, 40, 41
- Peritrophic membrane, 21
- Phallic rudiments, 41
- Phallobase, 40, 42
- Phallomeres, 41
- Phallosome, 40
- Phallotreme, 41
- Phallus, 40, 42
- Pharate period, 12, 15
- Pharynx, 2, 16, 23
- Phragmata, 34

- Plates, coxal, 44
 postnotal, 30
 segmental, 5, 6
 Pleural process, 30
 Pleural ridge, 30
 Pleurites, 6, 7
 Pleuron (pleura), 4, 6, 7,
 30, 34
 Podites, 3
 Postnotal plate, 30
 Postnotum, 34
 Postoccipital sulcus, 23
 Postocciput, 22
 Preoral cavity, 16, 23
 Prescutum, 30
 Prephragma, 30
 Pretarsus, 32
 Proctodaeum, 15, 16, 21
 Prognathous head, 24
 Prolegs, 32
 Prostomium, 25
 Prothorax, 28, 29
 Protocephalon, 25
 Proventriculus, 16
 Pupa (pupae), 11, 12
 Puparium, 12
 Pylorus, 16

 Recapitulation, 14
 Rectum, 16, 17
 Regenerative cells, 20
 Retromorphosis, 14

 Sagittae, 41
 Scape, 27
 Sclerites, 28, 34
 Sclerotization, 4, 5, 7
 Scutellum, 30
 Scutum, 30
 Segmental plates, 5
 Segmentation, 2
 abdominal, 36
 embryonic, 25
 head, 22, 26
 leg, 32
 primary, 3
 secondary, 3
 segment areas, 4
 Segments, 3
 Skeleton, grooves, 8
 Somites, 3
 Spinasterna, 31
 Spiracle, 31
 Sternellum, 30
 Sternites, 6
 Sternum (sterna), 4, 5, 6,
 8
 Stigmata, 31
 Stomodaeal valve, 16
 Stomodaeum, 15, 16, 21
 Striated border, 20
 Subgenal area, 22
 Subalare, 8, 34
 Sulcus (sulci), 5, 7, 8, 9,
 22

 Sutures, 2, 9
 Stylus (styli), 40

 Tarsomeres, 32
 Tarsus, 32
 Teloparamere, 40
 Tentorial bridge, 24
 Tentorium, 23, 24
 Tergites, 6, 7
 Tergum (terga), 4, 5, 6
 Thorax, 29
 Tibia, 32
 Trachea, 31
 Trochanter, 32
 Trochantin, 8

 Valves, 43
 Valvifers, 43, 44
 Valvulae, 43
 Veins, wing, 35
 Venter, 4, 6
 Ventral surface, 6
 Ventriculus, 16, 20
 Vertex, 22
 Vitellophags, 19

 Wings, 33
 Wing buds, 35
 Wing veins, 35

 Yolk cells, 18

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NUMBER 3

Roebbling Fund

SOLAR VARIATION AND WEATHER

A SUMMARY OF THE EVIDENCE, COMPLETELY
ILLUSTRATED AND DOCUMENTED

By

C. G. ABBOT

Research Associate, Smithsonian Institution



(PUBLICATION 4545)

62-65-21
CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION

OCTOBER 18, 1963

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NUMBER 3

Roebling Fund

SOLAR VARIATION AND WEATHER

A SUMMARY OF THE EVIDENCE, COMPLETELY
ILLUSTRATED AND DOCUMENTED

By

C. G. ABBOT

Research Associate, Smithsonian Institution



(PUBLICATION 4545)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 18, 1963

ABP
Gift
Public

PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

Roebling Fund

SOLAR VARIATION AND WEATHER

By C. G. ABBOT

Research Associate, Smithsonian Institution

From 1920 to 1955, with the aid of John A. Roebling, the Smithsonian Astrophysical Observatory under my direction, and later under that of L. B. Aldrich, made "solar-constant" observations from mountain tops in cloudless deserts in Africa, Asia, South America, and the United States. Although all the results were highly accurate, they were especially so from 1924 to 1944, for it was not till 1924 that the "short method" was fully perfected, and after 1944 the transparency of the atmosphere was less perfect than before.

From 1935 to the present I have sought to correlate the solar-constant measures with weather phenomena. I have published in Smithsonian Miscellaneous Collections¹ more than a score of papers on this subject. These papers and the volumes of the Annals of the Astrophysical Observatory, as well as several papers in outside journals, are referred to in the Appendix. They give in detail the evidence I shall rely upon in what follows.

I have been led to conclude firmly that variations of the sun's emission of radiation are associated intimately with weather changes. Since the death of H. H. Clayton I know of no professional meteorologists in the world, with the exception of Dr. Irving P. Krick, who have acknowledged support of my main conclusion. They all, indeed, credit us with highly accurate solar measurements, but in the absence as yet of connecting theory they distrust my proofs that solar variation has any considerable influence on ground weather.

Being now past 91 years of age, and firmly convinced that the sacrificing years of residence of my colleagues on high desert mountains have given to astrophysics and meteorology a long series of measurements of great practical importance, I feel compelled in jus-

¹ In the Appendix I give full references to all sources I refer to here. Nearly all are from Smithsonian Miscellaneous Collections. For brevity in the text I shall cite the Smithsonian publication number as "P." so and so.

tice to them to write a summary of the whole research. I hope to make it so thoroughly supported by varied evidences as to convince the professional scientists that it can no longer be ignored and allowed to sink into oblivion. But it is quite impossible for me to give half the evidence which saturates my mind with the certainty that the family of regular harmonics of 273 months, in solar radiation and terrestrial weather, is a controlling geophysical fact.

1. THE "SOLAR CONSTANT"

Pouillet invented his pyrheliometer, and about 1876, after measuring the heat of sun rays at different solar altitudes, he estimated that the instrument would have indicated 1.76 calories per square centimeter per minute if exposed outside the atmosphere at the earth's mean solar distance. Langley strongly argued that since the atmosphere transmits different wavelengths unequally, spectroscopic measures are necessary additionally to pyrheliometry to estimate the solar constant. He invented the bolometer for this purpose and used it at Allegheny Observatory and on and near Mount Whitney. Erroneous theory caused him to prefer 3.0 calories as the solar constant. K. Ångström, from solar measures on the Island of Teneriffe, attributing excessive influence to atmospheric carbon dioxide, preferred a value of 4.0 calories.

In volume 2 of *Annals, A.P.O.*,² is demonstrated the true theory for the spectrobolometric determination of the solar constant. An improved pyrheliometer similar to Pouillet's is described. Measurements at Washington, D. C., during the years covered by volume 2 indicated an average solar constant of 2.20 calories. A hint of solar variation appeared to be indicated by results of 1903 and 1904. By invitation of Director George E. Hale, we made measurements of the solar constant on Mount Wilson, Calif., in 1905 and 1906. From 1908 to 1920 the Smithsonian sent expeditions to Mount Wilson. A long-focus vertical telescope was installed in addition to solar-constant apparatus. Every day that solar constants were observed, the distribution of brightness over the diameter of the sun's disk was observed by allowing the 8-inch solar image from the telescope to drift without a clock over the slit of the spectrobolometer, in rays at various wavelengths. (See fig. 52, p. 62.)

In volume 3, *Annals, A.P.O.*, pages 21-29, a full description of solar-constant measurement is given. The silver-disk pyrheliometer

² We thus abbreviate Smithsonian Astrophysical Observatory.

is described on pages 47-52. More than 100 of these instruments have been constructed, standardized, and sold at cost by the Smithsonian Institution to observers in all parts of the world. For their standardization in absolute units, I devised the water-flow and water-stir absolute black-body pyrheliometers (see *Annals, A.P.O.*, vol. 3, pp. 52-69). With certain improvements, the water-flow double-barreled electrical-compensation pyrheliometer has been used for standardizing pyrheliometers hundreds of times. It is now recognized as the world's standard for measurements of solar radiation. The double-barreled water-flow design was suggested by V. M. Shulgin of Russia about 1927 and was immediately adopted by us.

About 1913, with F. E. Fowle and L. B. Aldrich, I did the original standardizations. We used thermometers certified in Paris and electrical instruments certified at the U. S. Bureau of Standards. Our solar measures from that time to this have always been expressed "on the scale of 1913." During the 40 years following, whenever improvements brought alterations we always made many checks and comparisons to keep the solar constant values still "on the scale of 1913." Observed solar-constant values have ranged irregularly from 1.900 to 1.960 calories and even higher. Their mean value "on the scale of 1913" is 1.944. We now recognize that the single-barrel standard pyrheliometer of 1913 in our hands gave values about 2 per cent too high. This was cured by the new instrument used since 1930. Various other important changes in solar-constant work have been made. These include restricting the sky exposure, making larger corrections for wavelengths beyond the violet and far in the infrared not observed daily, evaluating ozone absorption, determining personal equation, introduction of "the short method," and other changes. The effects of all these we have applied retroactively to all the solar-constant determinations from 1920 to 1955. (See *Annals, A.P.O.*, vols. 6 and 7.) Every published value was scrutinized extensively by L. B. Aldrich, Mrs. A. M. Bond, and W. H. Hoover, and generally by all three as a committee. So far as we have been able to bring it about, the solar-constant tables in volumes 6 and 7 of *Annals A.P.O.*, and also published in my papers P. 4088 and P. 4213, form a homogeneous series, all "on the scale of 1913."

Johnson, of the Naval Research Laboratory, using data from rockets, and with critical studies and use of our work, has published the solar-constant value 2.00 ± 0.04 calories.³ I doubt if any de-

³ Johnson, F. S. On the solar constant. *Journ. Meteorology*, vol. 11, No. 6, 1954.

termination depending basically on observing from mountain tops can claim with certainty to be within 1 percent of the absolute scale of heat. But as will be shown below, a series such as ours, where every effort was made to retain a constant scale over many years, can be depended on to preserve its *relative* homogeneity to 1/6 of 1 percent in daily values, even though 1 or 2 percent away from the true absolute scale throughout.

Volleys of criticisms of our solar-constant determinations were published between 1910 and 1914 by numerous authors. These we answered by several papers, but as they still continued we published (P. 2361) the extensive paper "New Evidence on the Intensity of Solar Radiation Outside the Atmosphere." This has three distinct parts:

(1) On September 20 and 21, 1914, two of the clearest and most uniform days ever experienced on Mount Wilson, we observed for the solar constant continuously from sunrise to 10 o'clock. This yielded for both days, by Langley's spectrobolometric method, solar-constant values computed as between air masses 1.3 and 4.0; 4.0 and 12.0; 1.3 and 20.0. All these six solar-constant measures (Langley's method) fell between 1.90 and 1.95, which shows both the excellence of the sky conditions and the accuracy of the observing.

(2) At Dr. A. K. Ångström's suggestion I designed, and our instrumentmaker Andrew Kramer constructed, five copies of an automatic combined pyrhelimeter and barometer. These were flown by balloons from Omaha by L. B. Aldrich, with the cooperation of Dr. William R. Blair and his assistants from the U. S. Weather Bureau, on July 11, 1914. One instrument was recovered uninjured in Iowa. It was calibrated both before and after flight under the same conditions of temperature and barometric pressure that obtained during flight. It rose to 24,000 meters, where 24/25 of the atmosphere lay below. It yielded a value of 1.87 calories, a value that lies within the limits of solar variation, as observed in those times at Mount Wilson, and as expressed on the Smithsonian "scale of 1913."

(3) Here I quote the concluding paragraphs of our paper:

It seems to us that, with the complete accord now reached between solar constant values obtained by the spectro-bolometric method of Langley, applied nearly 1,000 times in 12 years, at four stations ranging from sea level to 4,420 meters, and from the Pacific Ocean to the Sahara Desert; with air-masses ranging from 1.1 to 20; with atmospheric humidity ranging from 0.6 to 22.6 millimeters of precipitable water; with temperatures ranging from 0° to 30° C.; with sky transparency ranging from the glorious dark blue above

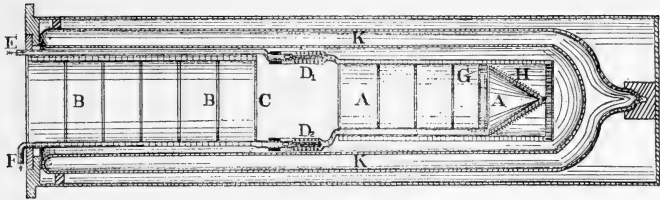


FIG. 1.—Water-flow standard pyrheliometer of 1913.

Mt. Whitney to the murky whiteness of the volcanic ash filling the sky above Bassour in 1912, it was superfluous to require additional evidence.

But new proofs are now shown in figure 10 [fig. 7, p. 10, of present paper]. This gives the results of an independent method of solar constant investigation. In this method the observer, starting from sea level, measures the solar radiation at highest sun under the most favorable circumstances, and advances from one level to another, until he stands on the highest practicable mountain peak. Thence he ascends in a balloon to the highest level at which a man may live. Finally he commits his instrument to a free balloon, and launches it to record automatically the solar radiation as high as balloons may rise, and where the atmospheric pressure is reduced to the twenty-fifth part of its sea level value. All these observations have been made. They verify the former con-

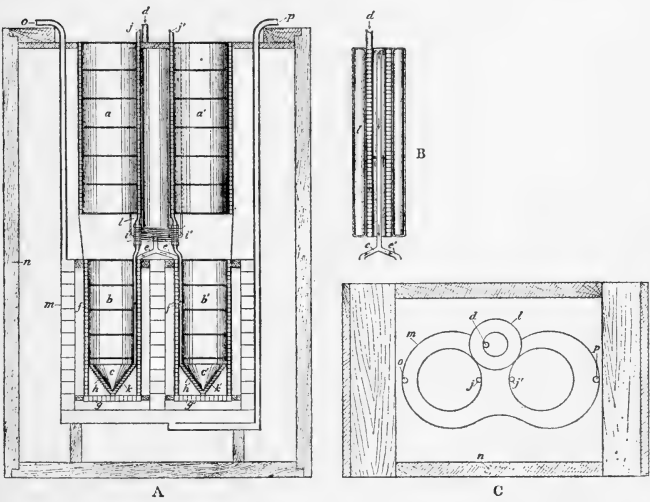


FIG. 2.—Double water-flow electrical compensation pyrheliometer.

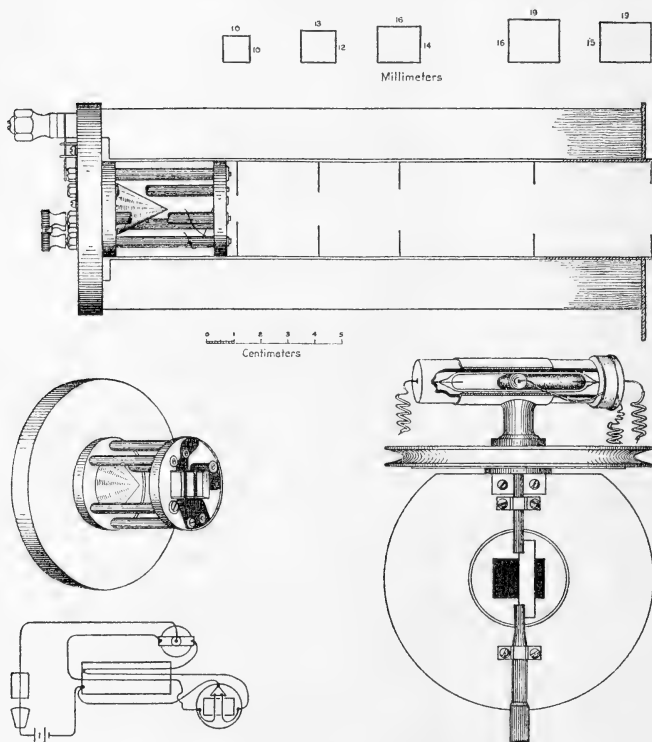


FIG. 3.—Ångström-Smithsonian pyrheliometer.

clusion; for they indicate a value outside the atmosphere well within the previously ascertained limits of solar variation.

The solar-constant method of Langley, which we used exclusively until 1920, is fundamental and sound. But it requires several hours of observation through unchanged transparency while the sun is ascending or descending, so that the thickness of air its rays traverse alters enough to give accurate transmission coefficients for all wavelengths observed. If during a morning series of measurements the atmosphere grows more transparent, the value obtained is too high, and *vice versa*. The opposite, of course, holds in the afternoon. We

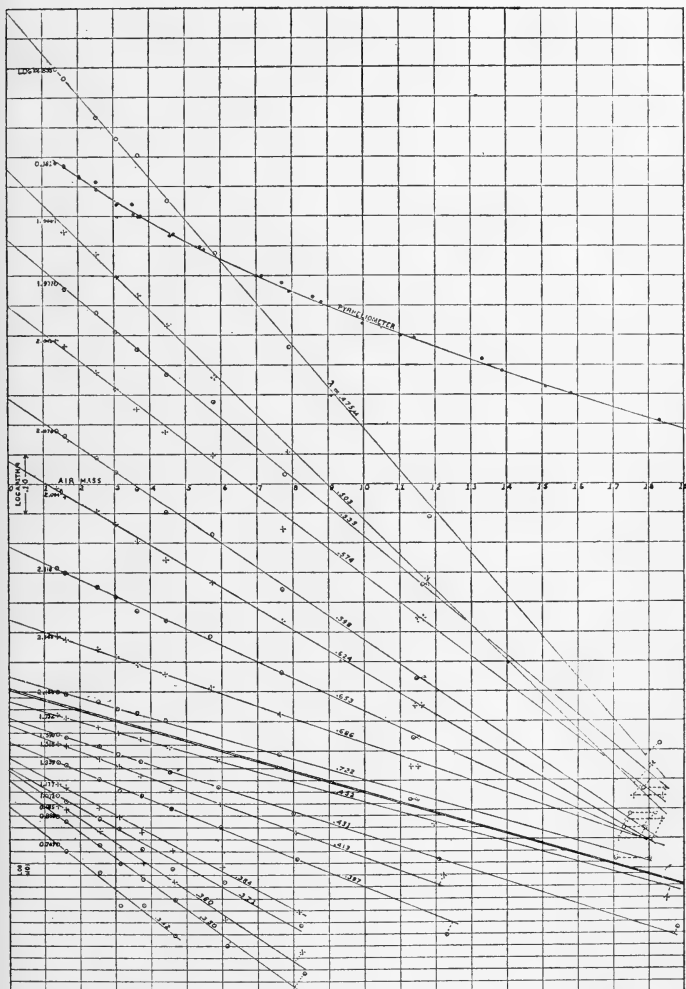


FIG. 4.—Logarithmic atmospheric transmission. Wavelengths 0.47 to 2.42 μ .

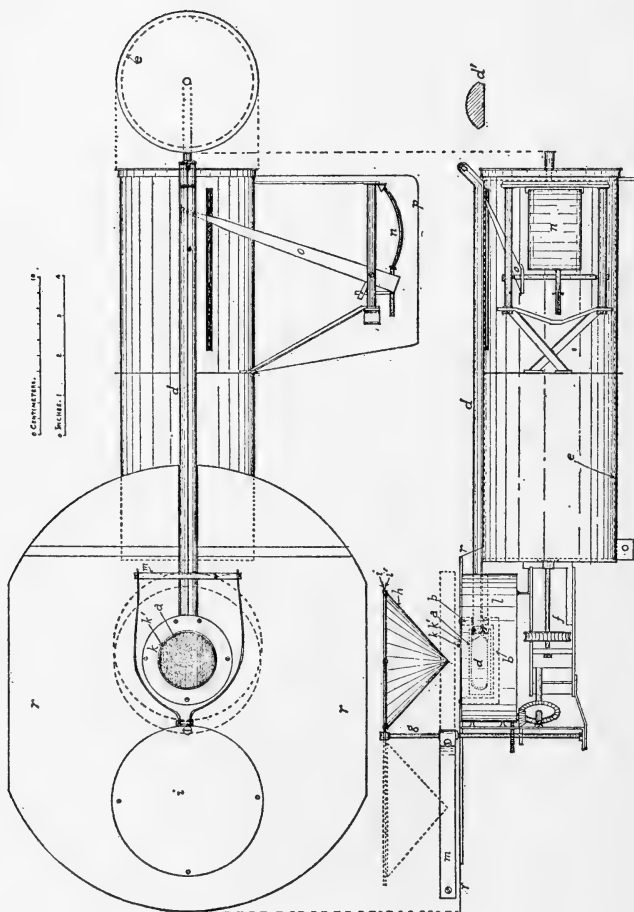


FIG. 5.—Recording balloon pyrheliometer.

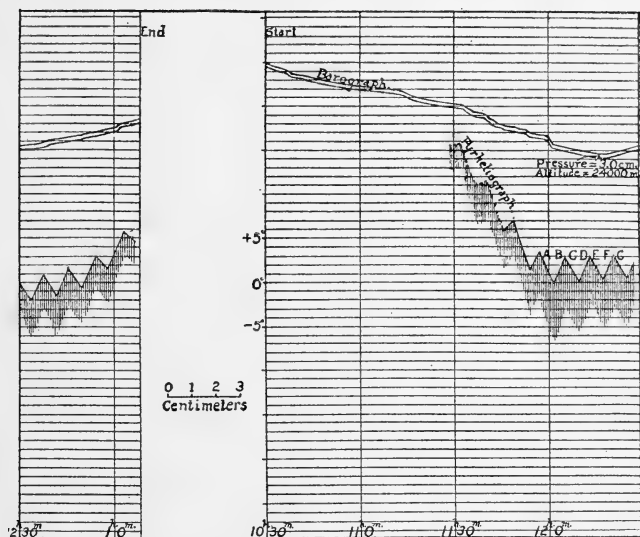


FIG. 6.—Record pyrheliometry to 15 miles altitude.

wished to devise a method whereby several values of the solar constant could be obtained per day, by intervals of observing too short for hurtful changes of transparency.

2. THE SHORT METHOD

Alfred F. Moore, observing at Calama, Chile, showed me in 1920 a long series of observations with our sky-radiation instrument, the pyranometer (fig. 9, p. 13), on the brightness of a limited zone of sky surrounding the sun. When the transparency of the atmosphere is low, the sky gets brighter, and *vice versa*. Comparing Moore's pyranometry with simultaneous determinations of atmospheric transparency at 40 wavelengths, made by Langley's method, I was able to draw families of curves throughout the spectrum of the sun, giving transmission coefficients suited to all states of sky brightness at Calama. (fig. 8, p. 11).

This is the basis of the "short method" of solar-constant observing. It requires only about 10 minutes of observing by spectrobolometer, pyranometer, and pyrheliometer. We became accustomed to making

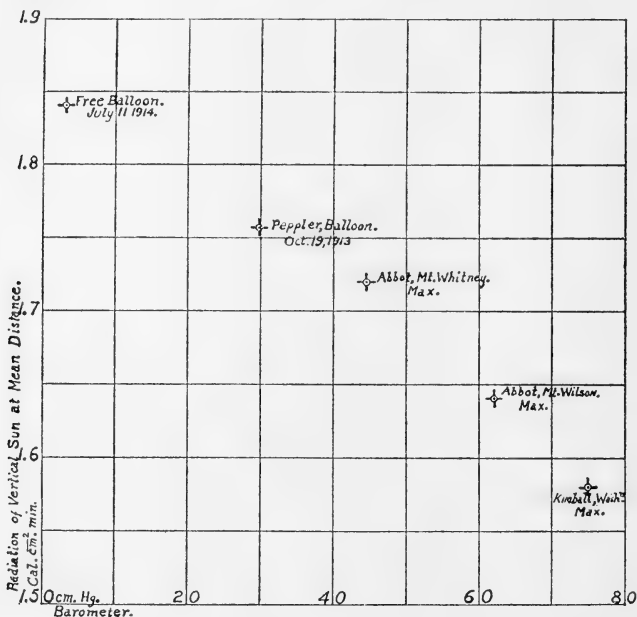


FIG. 7.—Maximum pyr heliometry, sea level to 15 miles altitude.

three or even five determinations of the solar constant per day and could utilize days with cumulus clouds intermittently—days quite unfit for Langley's method. The short method is, indeed, empirical and must be set up separately for each observing station by observing a year or more simultaneously with Langley's method to standardize it. We continually improved the "short method" till 1926, but after that we used it exclusively except for occasional checks by Langley's method.

3. ACCURACY OF "SHORT METHOD" SOLAR CONSTANTS

In volume 6, page 163, *Annals*, A.P.O., are compared the solar constants observed on 616 identical days at Mount St. Katherine in Egypt and Mount Montezuma in Chile. Winter at one station corresponds with summer in the other. The difference between daily results ranged from 0 to 0.028 calorie. The weighted mean differ-

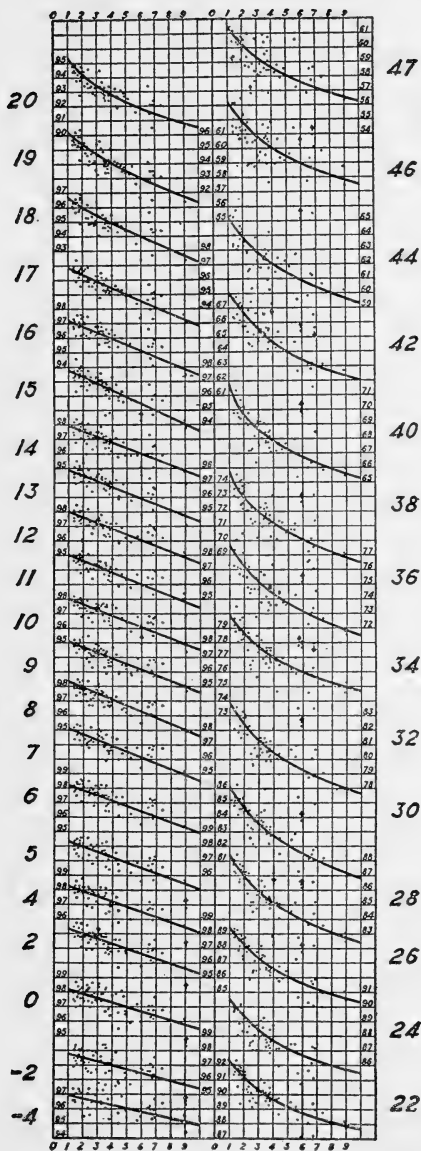


Fig. 8.—Atmospheric transmission by short method.

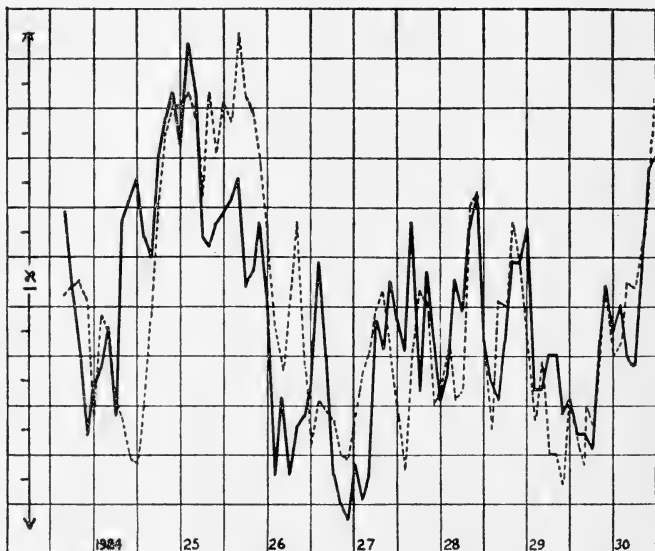


FIG. 8a.—Solar constant measures repeat after 273 months.

ence for 616 days is ± 0.0076 calorie. In 1953, Mrs. L. S. Hill made several similar comparisons. Mount Montezuma, Chile, is compared with Table Mountain, Calif., and with Tyrone, N. Mex. Table Mountain is compared with Tyrone. Her data cover, respectively, 891, 283, and 202 identical days.

From this abundant evidence, with no indication of appreciable seasonal influence, I confidently take the average probable error of one day's observation at one station by the "short method" to be $1/6$ of 1 percent of the solar constant.

In volumes 6 and 7, *Annals, A.P.O.*, are published about 6,000 daily values of the solar constant obtained by the short method, often by two or three stations observing upon the same day. Fully half of them are "very good" and at least as accurate as those referred to in Table 1. The *mean* value for *one month* would rest on at least 10 of them, and frequently 20 to 30. The *month* will be the unit I shall use in the discussion to follow. Its probable error can justly be regarded as $1/\sqrt{10} \times 1/6 = 1/20$ of 1 percent of the solar constant.

TABLE 1.—Accuracy of solar observations

Station Pair	Mean difference Calories ÷ 10,000	Number of comparisons
Montezuma—Table	76.8	891
Montezuma—Tyrone	79.6	283
Montezuma—Mount St. Katherine.....	76.0	616
Table—Tyrone	77.9	202

In tabulations which we make of forms and amplitudes of harmonic solar variations, these range from 4 to 91 months in periods. Results on the solar-constant periods rest on mean values of tabulations of between 10 and 100 months, their numbers increasing as their period decreases. So the individual points on a periodic curve computed from monthly values will have probable errors ranging from $1/20 \div \sqrt{10}$ down to $1/20 \div \sqrt{100}$ of 1 percent of the solar constant.

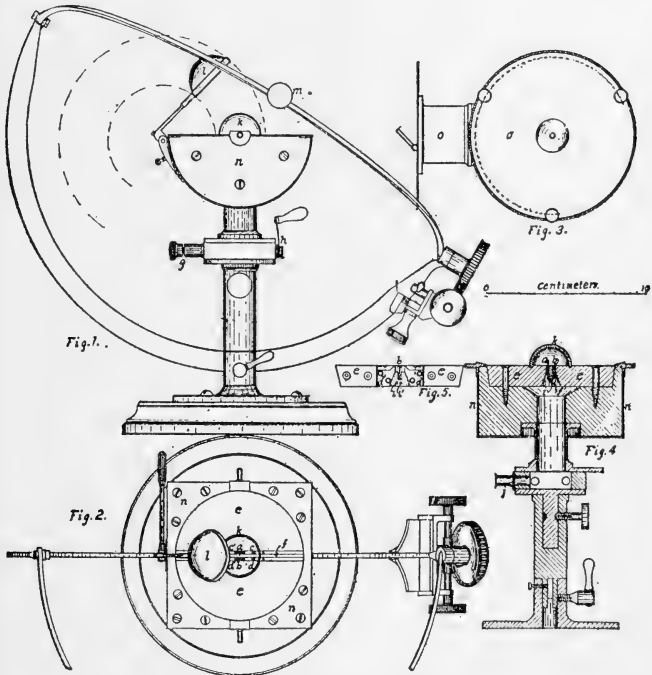
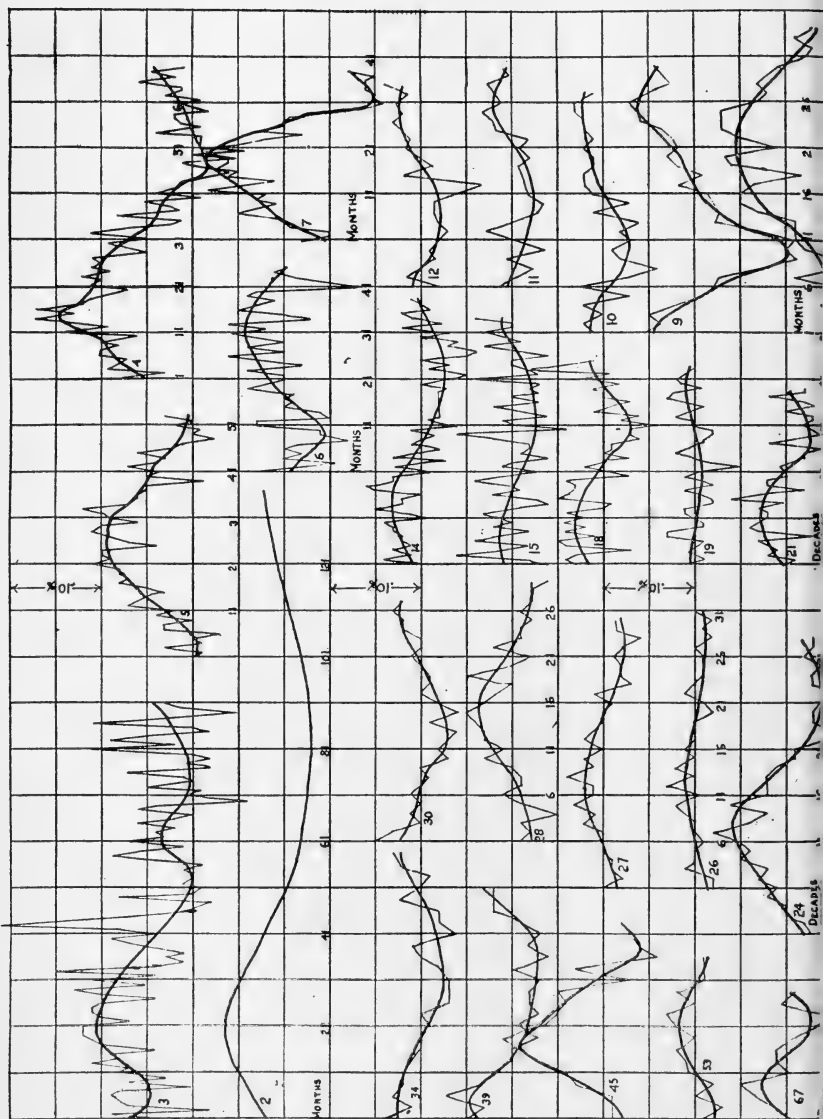


FIG. 9.—Smithsonian pyranometer.



The smoothed curves representing the periods, as will appear from figure 10, are nearly sine curves. Their regular shapes, of course, make them stronger evidences of real variation than their individual points. But these points, as just said, have probable errors ranging from $1/60$ to $1/200$ of 1 percent of the solar constant.

4. PERIODICITIES IN SOLAR VARIATION

Over 25 years ago I noticed periodic repetitions of dentlike depressions in graphs of the solar-constant record. These periods appeared to be harmonics of 273 months. Notably appeared 273/7, 273/21, 273/39. In my paper "Periodic Solar Variations" of June 1955 (P. 4213) I amplified what I had said earlier (P. 4088) in May 1952. For convenient tabulation I gave in the two papers together the departures from 1.90 calories of all mean monthly solar constants from August 1920 to December 1952. These departures are expressed as percentages of the solar constant. Thus the computer uses small positive numbers exclusively, and his results are expressed as percentages of the solar constant, taken as 1.944 calories per square centimeter per minute.

P. 3902 graphs the march of the solar constant from 1920 through 1951 and shows that it is closely represented by the summation of 23 periods, all exact harmonics of 273 months. To be sure, in 1922 and 1923 there is a depression far exceeding any observed since. Perhaps it represents one member of another family of solar changes of long periods. Unfortunately, since 1955 no measures of the solar constant have been made so far as I know. In P. 4462, of 1961, I suggest that the solar constant might be observed daily with higher accuracy than ours from a satellite. That might reveal solar changes of great importance in future years. Figure 8a, p. 12, shows the solar constant repeating after 273 months.

Figure 10 graphs 26 harmonic periods in solar variation. They are cleared of overriding subharmonics. Small type numbers give the length numbers of the 26 harmonics as fractions of 273 months. All the curves have approximately sine form. Table 3 of P. 4213 tabulates the amplitudes of the periods and of their submultiples which were removed for the sake of clearness. Altogether 31 harmonic periods are given in this table with amplitudes ranging in solar radiation from 0.18 down to 0.02 of 1 percent. Small as they are, all these amplitudes are far above the probable errors derived in Section 3.

To show the importance of clearing away the overriding submultiple periods, figure 11 is a graph of the period of 39.0 months recently

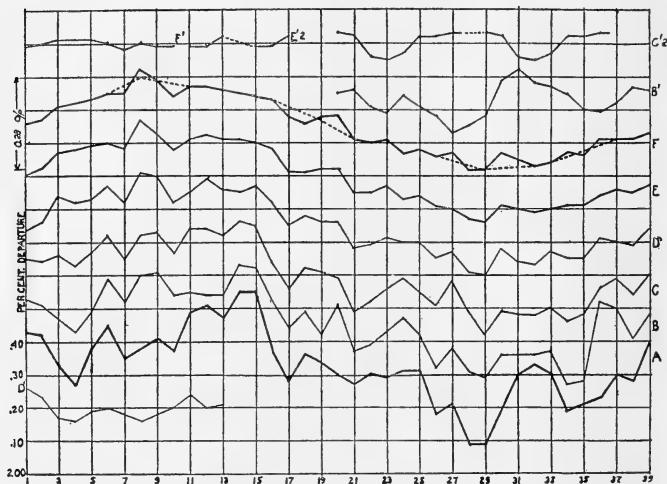


FIG. 11.—Thirty-nine-month period in solar variation cleared of shorter harmonics.

computed, using *all* the solar constant measures from the years 1923, January, through 1943, June. Periods 273/14, 273/21, 273/28, 273/35, 273/91 (and 273/24 doubtful) are shown successively removed by computation and are exhibited as graphs B', C', D', E', F', leaving curves B, C, D, E, F. This leaves 273/7 almost fully cleared of irregularities. It is a very pretty sine curve with amplitude 0.28 percent of the solar constant.

5. ANOTHER TYPE OF PERIODIC VARIATION DUE TO SOLAR ROTATION

The late Dr. H. Arctowski published (Proc. Nat. Acad. Sci., vol. 26, pp. 406-411, 1940) graphs (here fig. 12) which show variable differences in brightness over the sun's rotating surface associated with corresponding variation of the solar constant. Figure 13 shows solar-constant results, March to April 1920. A huge sunspot group passed centrally over the sun's disk March 20-24 (see fig. 13). It produced a large depression of the sun's radiation. L. B. Aldrich gave extensive evidence (Smithsonian Report for 1952) proving the increase of solar radiation with increased sunspot activity (see fig. 14).

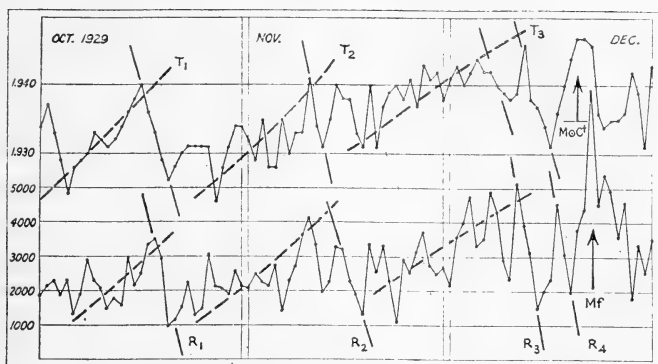


FIG. 12.—Relationship of calcium flocculi and solar constant as demonstrated by Arctowski

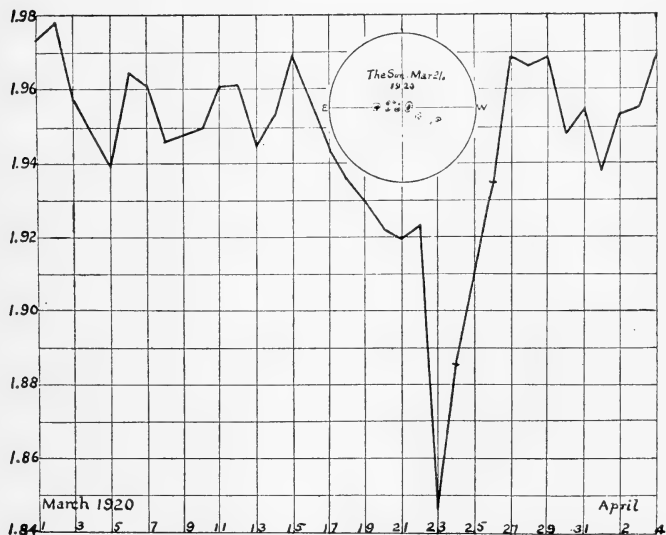


FIG. 13.—Huge sunspot central group of March 1920 depresses sun's radiation.

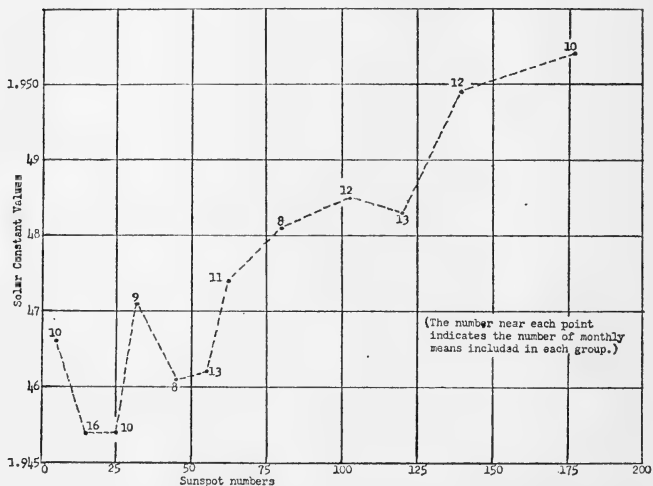


FIG. 14.—Solar radiation increased by rising sunspot activity as shown by Aldrich.

When very great sunspot groups are *exactly* central on the solar disk, however, solar radiation decreases (see fig. 13). Again, from P. 2499, I reproduce in figure 15 results of correlation coefficients computed over an interval of 40 days. These show that in 1915 the solar rotation, with its 27-day period, brought up changes of correlation, between the days of solar-constant measures and the days following, which ran through a range of 50 percent in correlation. They passed from +20 through 0 to -30 percent in correlation coefficients.

Though the event is not of periodic nature, I mention here P. 3916 and P. 3940 which show, respectively, the sharp fall in the solar constant when West Indian hurricanes or great magnetic storms are reported (see figs. 16 and 17).

6. SOLAR VARIATION AND WEATHER

Having explored above evidence on the intensity of solar radiation and on the variability of it, I now take up the subject of the influence of solar variation on terrestrial weather. I will first quote from my paper "Solar Variation a Leading Weather Element" (P. 4135, Aug. 1953): "On January 28, 1953, the American Meteorological Society devoted the day to consideration of the influence of solar variation on

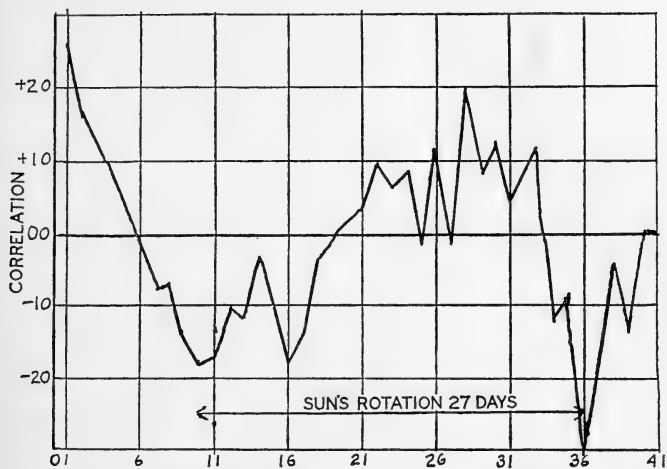


FIG. 15.—Sun's rotation in 27 days shown in 1915 solar-constant correlation.

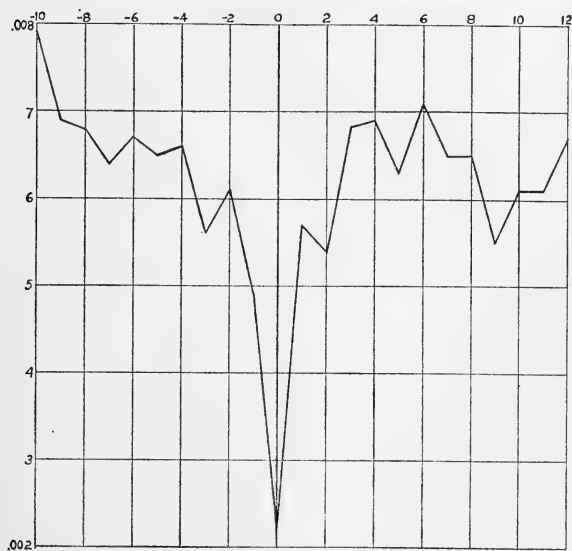


FIG. 16.—Solar constant and West Indian hurricanes.

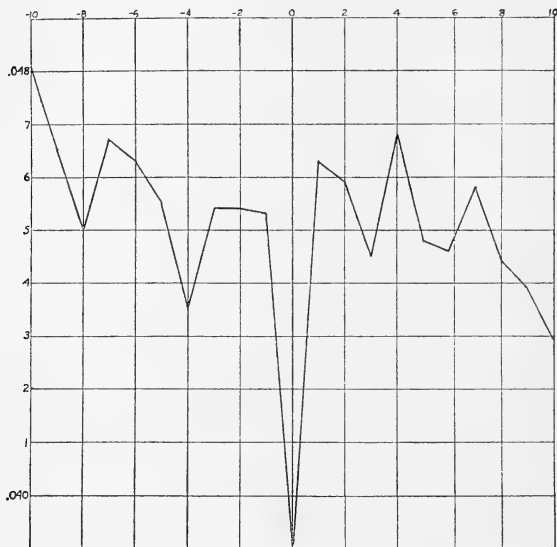


FIG. 17.—Solar constant and severe magnetic storms.

weather. An early speaker said he acknowledged the results of long continued studies of total solar variation, which had been made, as probably sound. But the variations found appeared to be of the order of 1 percent, or much less. No reasonable theory could show that these might have important weather influences. He distrusted statistical conclusions unless grounded on sound theory. Statistics might show that it is dangerous to go to bed, for a great majority of decedents die in bed." The panel appeared to agree unanimously with him, for nobody supported the view that solar variation is an important weather element.

In Section 4, above, I show that a family of periods, exact harmonics of 273 months, exist in *solar variation*. In Section 3 I show that the solar constant measurements are *abundantly accurate enough* to support this fact. In figures 10 and 11 I show in many members of this harmonic family, how the shorter periods overlies and confuse the graphs of the longer ones, and how the shorter ones are computed and removed, leaving the longer ones as approximately sine forms.

I now show in figure 18 exactly similar treatment of the 39-month

period in the *precipitation* at Vienna, Austria. Jonathan Wexler computed electronically for us the 39-month period in Vienna precipitation in terms of average percentage departures from the normal for all months between 1910 and 1950. I select the months when Wolf sunspot numbers exceeded 20. In our adopted nomenclature this group as presented from 1910 to 1950 is Category 2, Division 2. This means that the Wolf sunspot number was above 20 and the time interval was the second half of the years spanning 1870 to 1950.

When one scans line A, figure 18, it naturally divides into halves. The average half, line B', is computed and subtracted, leaving line B. From this the average third, line C', is removed, leaving line C. From this, successive removals are D', one-fifth, leaving line D; then E', one-eleventh, leaving line E; and finally F', one-thirteenth, leaving line F. The line F shows a nearly smooth sine curve. The small indentations may all be traced to accidental irregularities of precipitation in the original observations. The amplitude of sine curve F is 17 percent of normal precipitation, which is $17/0.28$, or about 60

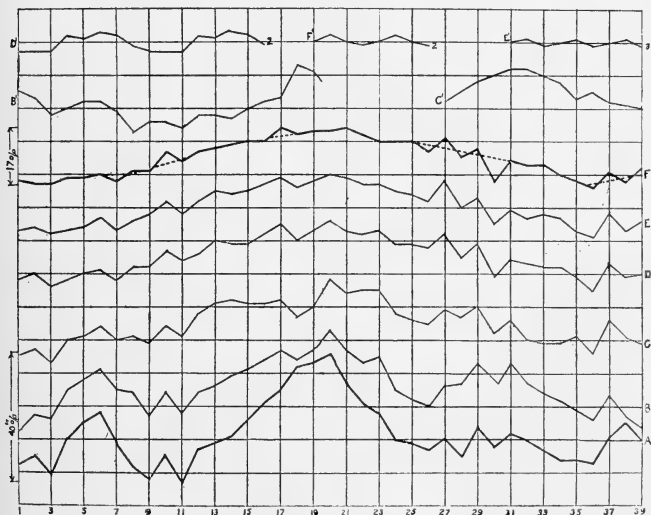


FIG. 18.—Thirty-nine-month period in Vienna precipitation, cleared of shorter harmonics.

times as great as the amplitude of sine curve line F (fig. 11), is in percentage of the solar constant.

I will now give in figures 19 and 20 two more examples from our study of the period 273/9, or 30-1/3 months, in the precipitation of Buenos Aires, Argentina. Tables 2 and 3 of Figure 19 are from a direct photograph of Jonathan Wexler's electronic computation of Category 1, Divisions 1 and 2, for the period of 30-1/3 months.⁴ Taking first Division 1, Mrs. Hill's graph (fig. 20) from Wexler's means discloses an obvious overriding period of 273/18. Removing this as usual, the curve remaining discloses 273/27. After this I removed 273/45, then 273/63. This left a nearly smooth sine curve, 273/9, of about 30 percent amplitude, with minimum at the fifth, and maximum at the twentieth month.

⁴ As shown on figure 19 we arbitrarily cut down precipitation when very high to 200 percent normal.

PRECIPITATION BUENOS AIRES, ARG. FRACTION TABLE 30 AND 1/3 MO.											
DIVISION 1 TABLE 2						DIVISION 2 TABLE 3					
1876 JUL	1886 SEP	1889 MAR	1899 APR	1901 NOV	MEANS	1909 JUN	1911 DEC	1922 JAN	1932 MAR	1942 APR	MEANS
88	69	175	98	91	104	104	164	93	66	70	99
95	90	120	98	77	96	110	158	108	80	56	102
86	103	114	104	59	93	120	174	97	127	75	119
88	67	115	86	63	84	135	156	102	138	81	122
66	52	88	81	72	72	103	138	127	133	81	116
67	63	81	103	72	77	95	147	185	146	91	133
69	41	74	95	70	70	87	145	172	124	93	124
66	68	76	82	62	71	88	126	180	80	51	105
101	82	81	118	56	88	69	112	160	79	42	92
107	91	87	169	48	100	67	135	118	100	48	93
146	91	102	150	64	111	45	143	57	93	34	74
137	103	106	177	91	123	49	112	64	109	58	78
115	74	83	203	107	117	46	104	64	115	87	83
83	79	73	222	110	109	66	90	75	97	106	87
81	71	94	172	121	108	78	82	75	71	92	79
65	109	84	221	117	115	88	90	87	54	111	86
104	105	76	221	87	122	72	100	91	58	102	85
114	113	78	221	122	129	67	107	112	60	85	86
142	95	72	182	124	123	69	97	102	72	87	86
147	95	55	181	151	126	50	97	114	86	132	96
127	52	46	145	157	106	75	99	113	95	140	104
102	75	56	117	155	101	103	138	109	75	141	113
102	95	73	92	107	94	115	138	83	86	147	114
84	107	77	97	106	94	110	153	113	77	150	121
91	122	90	74	65	88	123	144	113	75	110	113
83	149	111	50	62	91	92	123	98	110	84	101
85	192	143	49	94	113	97	139	89	124	70	104
86	182	174	70	106	124	101	161	83	98	73	103
66	185	171	77	89	117	145	156	39	122	93	111
60	196	160	83	92	118	165	184	33	118	94	119
65			94					63			

FIG. 19.—Electronic tabulation of precipitation at Buenos Aires, 30½-month period.

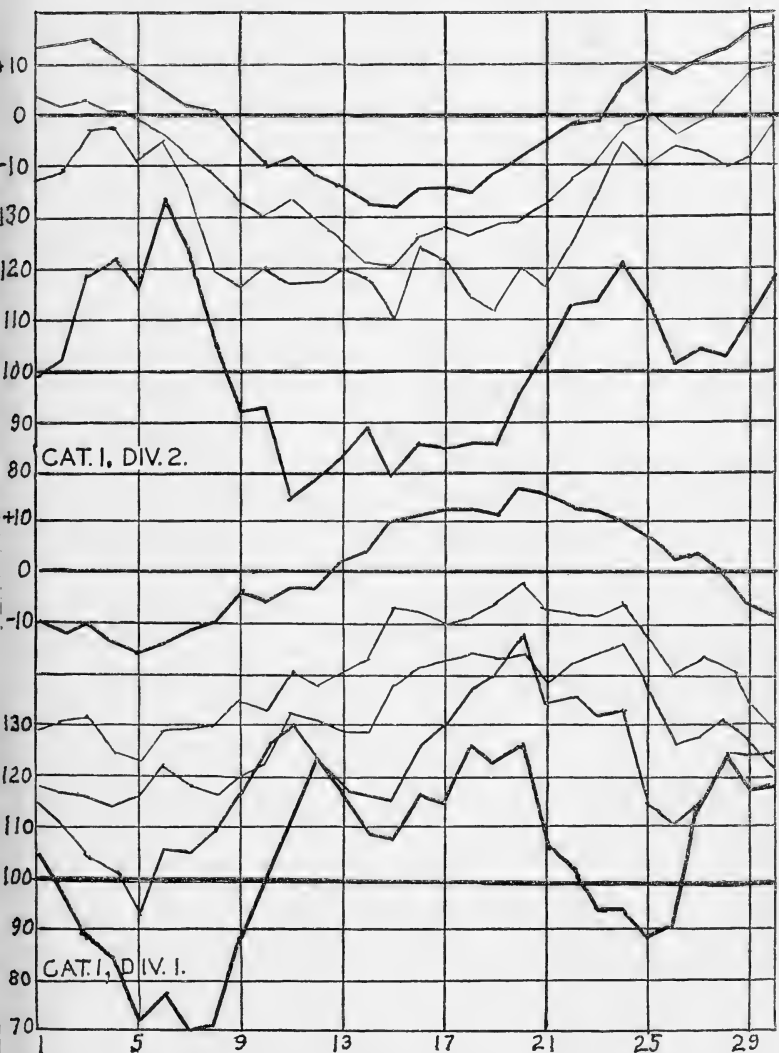


FIG. 20.—Buenos Aires precipitation, 30½-month period, cleared of shorter harmonics.

Turning to Category 1, Division 2, I first remove 273/18, then 273/45. After removing these overriding submultiple harmonics, 273/18, 273/45, there is left only the nearly smooth sine curve 273/9. The amplitude of this final curve for Category 1, Division 2, is 34 percent of normal rainfall at Buenos Aires. This percentage is 160 times the percentage of the normal solar-constant radiation given as 0.21 percent in P. 4213 (here fig. 10) for the period 30-1/3 months.

In further emphasis on the existence of subharmonics preventing direct recognition of the longer periods, while disclosing shorter ones otherwise hidden, I refer to eight telling cases: P. 4103, p. 4; P. 4352, pp. 6, 8, 11; P. 4390, p. 12.

7. LONG-RANGE FORECASTING OF WEATHER

As yet theory fails to explain why the family of harmonic periods related to 273 months, which exists in the sun's variation of radiation, should exist also with identical periods in precipitation and temperature on earth. Still more surprising, the weather amplitudes have frequently a hundred times the percentage apparent importance of the identical periods present in solar-constant measures. But a huge body of measurements accumulated over 40 years, including detailed study of weather in 54 cities, proves that it is so. The periods in weather, to be sure, are hidden from casual view because though invariable in solar radiation (P. 3893, p. 22, figs. 11), *their phases vary* with place, time of the year, prevalence of sunspots, and growth of population. All these things alter atmospheric transparency and thereby *shift times of terrestrial response to solar causes*. But when long-time weather records are grouped with attention to eliminating as far as possible all these disturbing influences, and are cleared of overriding shorter harmonic periods, *the identical periods* observed in solar-constant measures *stand out clearly in weather records all over the world* as sine curves.

In view of all these facts, may it not be possible to forecast rainfall and temperature by adding together the amplitudes of these weather periods? This would require that the forms and amplitudes which the periods presented in past years, and the disturbances of their phases due to the causes mentioned above, would all remain sufficiently constant.

We have made at 54 stations tests of such long-range weather forecasting. On the whole the results have been very encouraging. Ex-

amples will show both excellent successes and disappointing partial failures.

About 10 years ago, working quite alone from the beginning with "World Weather Records," and computing myself every succeeding step, I began the study of the precipitation at St. Louis, Mo. This research occupied me for over three years and resulted encouragingly beyond expectation (see P. 4211). It was early discovered that the normal monthly values, customarily published with long monthly weather records, must be recalculated in two parts, one for low, the other for high sunspot numbers (P. 4090). Sunspot activity makes a very important difference, both in the magnitudes and in the yearly run of monthly means. This obtains both for precipitation and temperature. After inspecting the curves of Wolf sunspot numbers, it seemed best to set the boundary between low and high sunspots at 20 Wolf numbers. We have thus far studied 54 stations, using "World Weather Records" (now published up to 1950). These records that we have used have been electronically recomputed by Jonathan Wexler to give normal monthly values for sunspots ≥ 20 Wolf numbers. The observed monthly values are all reduced to percentages of these new sets of normals.

In order to eliminate as far as practicable the shifting of phases attending time of the year, periods less than $15\frac{1}{6}$ months are separated into three groups. These are: January-April; May-August; September-December. There are two series of these groups, one for sunspots less than 20 Wolf numbers, and the other for sunspots above 20 Wolf numbers. As we see, exaggerated conditions as "smog" in Los Angeles County, Calif., the multitudes of automobiles, airplanes, factories, and forest fires which have attended the increase of population have greatly altered atmospheric transparency and thereby have shifted phases. We imperfectly allow for this by dividing the whole interval of records, say 1870-1950, into halves.

So, up to the period $15\frac{1}{6}$ months, consideration of the (3 parts of the year) \times (2 ranges of Wolf numbers) \times (2 halves of the record interval) yields 12 groups of records for each period. Dropping the 3 divisions of the year, from $18\frac{1}{5}$ to $45\frac{1}{2}$ months there are 4 groups for each period. For the last 3 periods, $54\frac{3}{5}$, $68\frac{1}{4}$, and 91 months, we drop the halving of the time interval, and retain only separation of ≥ 20 Wolf numbers. Altogether we separate the record into $(12 \times 15) + (4 \times 9) + (3 \times 2) = 222$ groups. This separation would restrict many groups to too few members to deserve confidence. So we make the assumption that, though different individually in

phases, the groups of the same Wolf number will be approximately of nearly the same form of distribution, and amplitude of intensity, and may be combined. But if combined, the individual phases must not be lost sight of. So when six columns of means are averaged to yield one general mean, the columns must be shifted bodily upward or downward to be as nearly as possible in the same phase. We use symbols, ok, \uparrow_m , \downarrow_n , to indicate shifts. Then the general mean column of the six numbers must be shifted back to the original phase relations of its individual members when tabulated for the summation to make up a forecast.

Beyond 15-1/6 months period, practically every period when plotted betrays confusion, for shorter harmonic periods override the period sought. This requires what is by far the most arduous computation of all. After the electronically prepared tables are received from Mr. Wexler they must be treated as was seen in figure 18 to clear the overriding shorter harmonics away. It is sometimes difficult to decide which submultiples are present until after one or two futile trials. Such repeated trials with periods 54 to 91 months in length are very tedious.

The combination of 6 member columns into a general mean, as we do for periods less than 15-1/6 months, will best be understood by a numerical example. The letters a, b, c denote, respectively, data of January-April; May-August; September-December. Subscripts 1 and 2 with them mean first and second halves of the records. As expected, these columns are not in the same phase. The signs, ok, \uparrow , and \downarrow , show how much the columns must be moved up or down bodily to be brought into the best posture for uniform phases. When the mean percentage departures from normal in the final column of table 5 are used in the summation for prediction, the columns marked "ok" are to be replaced by the general mean column *without shifting*. The general mean values are to be *lowered* 2 months

TABLE 4.—*Berlin. Period, 7.0 months*
Wexler's table. Means

Cat. 2, Div. 1					Cat. 2, Div. 2						
a ₁	ok	b ₁	↑ ₂	c ₁	ok	a ₂	↑ ₂	b ₂	↓ ₂	c ₂	ok
94		96		93		114		94		100	
97		100		96		105		97		100	
99		99		96		103		105		101	
99		95		91		100		109		97	
99		99		94		105		109		97	
99		95		101		103		115		89	
95		91		95		109		112		98	

TABLE 5. *Berlin. Period, 7.0 months.
Rearranged table with symbols unchanged.*

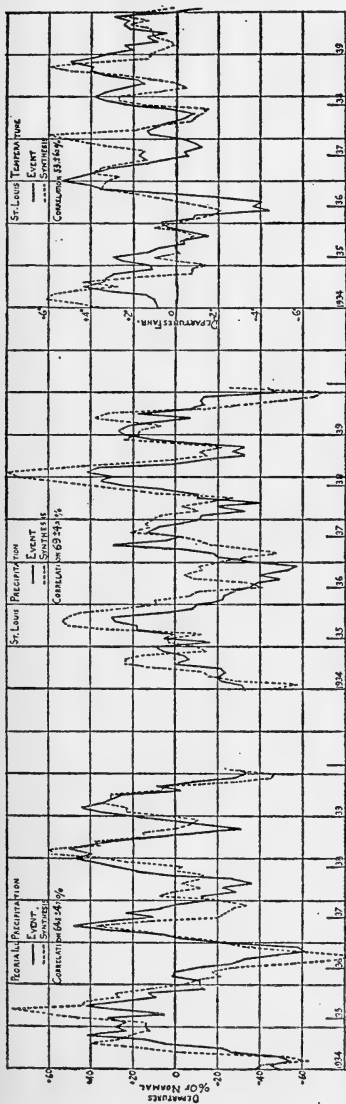
Cat. 2, Div. 1								Cat. 2, Div. 2						General mean ÷ 6
a ₁	ok	b ₁	↑ _a	c ₁	ok	a ₂	↑ _a	b ₂	↓ _a	c ₂	ok	Sums Σ		
99		99		93		109		109		100		+9	+1	
99		95		96		114		115		100		+19	+3	
99		99		96		105		112		101		+12	+2	
98		95		91		103		94		97		-22	-4	
94		91		94		100		97		97		-27	-4	
97		96		101		105		105		99		+3	+0	
99		100		95		103		109		98		+4	+1	

at b_1 , *raised* 3 months at b_2 , and *lowered* 3 months at a_2 , so as to be in proper phases in the summation. As for the modification of results in periods from 18-1/5 to 91 months, examples of the removal of overriding submultiples are given in figures 11, 18, and 20.

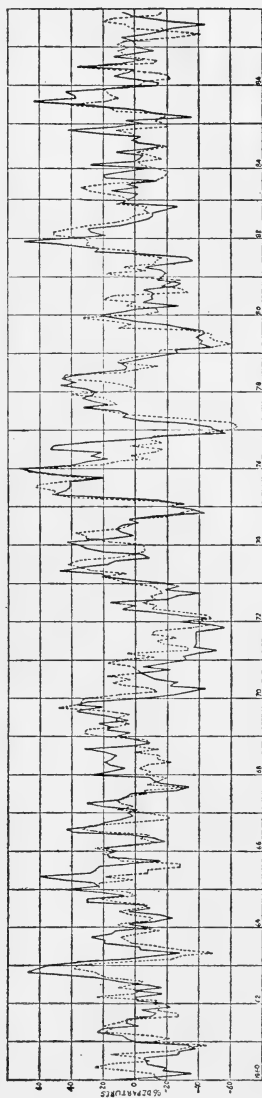
8. EXAMPLES OF FORECASTING

Figure 21 is from a direct photograph of my work when computing alone, beginning from "World Weather Records," 1854-1939, and finally forecasting St. Louis precipitation, 1875-1879. (See P. 4211.) All the records, 1854-1939, of precipitation at St. Louis were used to fix every individual year. Every year computed, therefore, is equally as really a forecast as if it were after 1939 and stems from zero year (the median) 1895. The forecast gives a correlation coefficient of +80 percent for the 5 years 1875 to 1879 between forecast and observation. Figure 22a, which includes Figure 21, is also a direct photograph from my comparison of forecast and event from 1860 to 1887. Throughout this interval there is an average correlation coefficient of 70 ± 10 percent. Figure 22b gives direct photographs of results I obtained from forecasts of precipitation and temperature during the interval 1934 to 1939 for St. Louis and Peoria. I employed *all* records for the period 1854-1939 to fix the forms and amplitudes. In all these examples just given the departures in forecasts and events, in short all the computation, is done with 5-month consecutive means.

The reader will see that since *all* records, 1854-1939, were used impartially to fix every number forecasted or backcasted in figures 21 and 22 and beyond, the number of years forecasted forward or backward is to be determined as *starting at zero* for the year $(1939 + 1854)/2 = 1896$. Hence, the forecast of St. Louis precipita-



b



a

FIG. 22a, b.—Forecast of St. Louis precipitation, 1860-1887; forecasts various, 1934 to 1939.

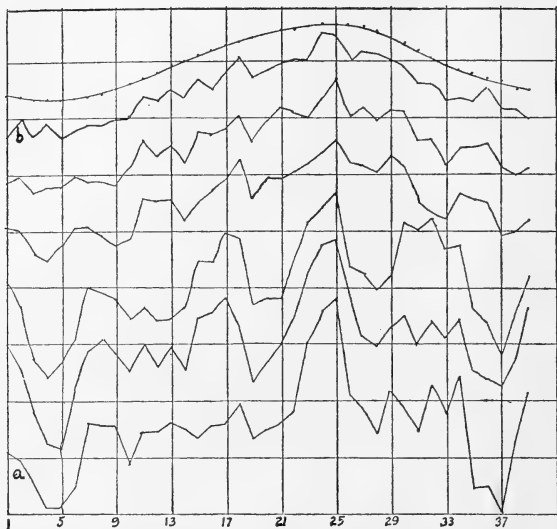


FIG. 23.—Precipitation, Helena, Mont., 39-month period, cleared of shorter harmonics.

tion for the year 1956 in P. 4211 is a “60-year forecast,” as claimed by the title of P. 4211.

I will conclude these illustrative examples by graphs (see figs. 28-37)⁵ taken from P. 4390 and P. 4471 on precipitation and temperature forecasted or backcasted from data smoothed by 3-month consecutive means using *all* the records from about 1870 to 1956. It will be seen that forecasts and events have about equal amplitudes. They evidently exhibit the same principal features. Principal and even minor features in prediction and event prevailingly coincide on the same months. But sometimes there are displacements of 1, 2, 3, or

⁵ Figure 33 was prepared from the 1,032 months of records used in P. 4390, “A Long-range Forecast of United States Precipitation.” These records covered the years 1870-1956 and centered on the year 1913. *All* 1,032 months of these records had *equal weight* in the forecasts. The observations quoted in figure 33 were not available till late 1960. Figure 33 was used as a slide at my National Academy paper of April 1961. Whatever success it has is for being a verification of forecasts of precipitation for 14 cities from a *zero date* of 1913, 46 years previous to 1959.

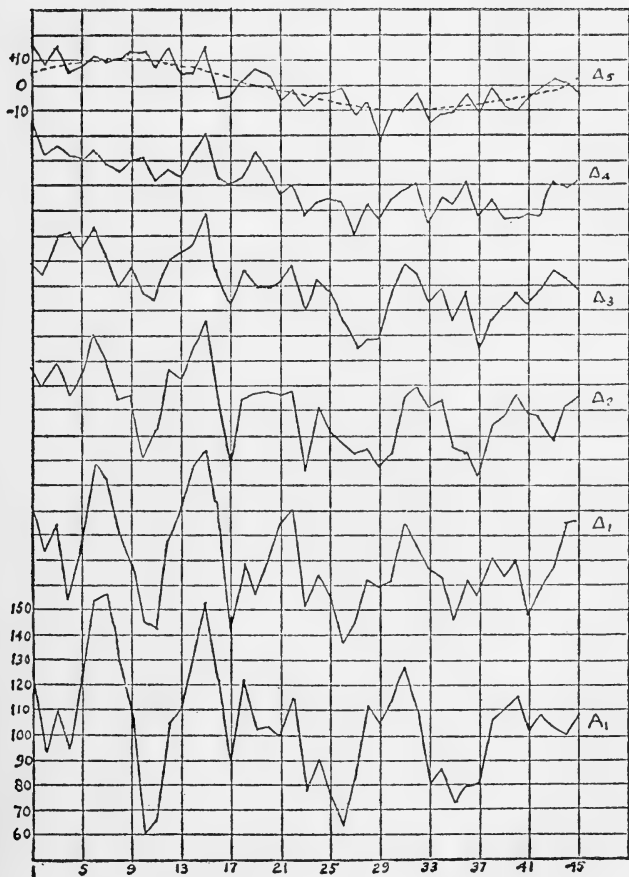


FIG. 24.—Precipitation, Natural Bridge, Ariz., 45½-month period, cleared of shorter harmonics.

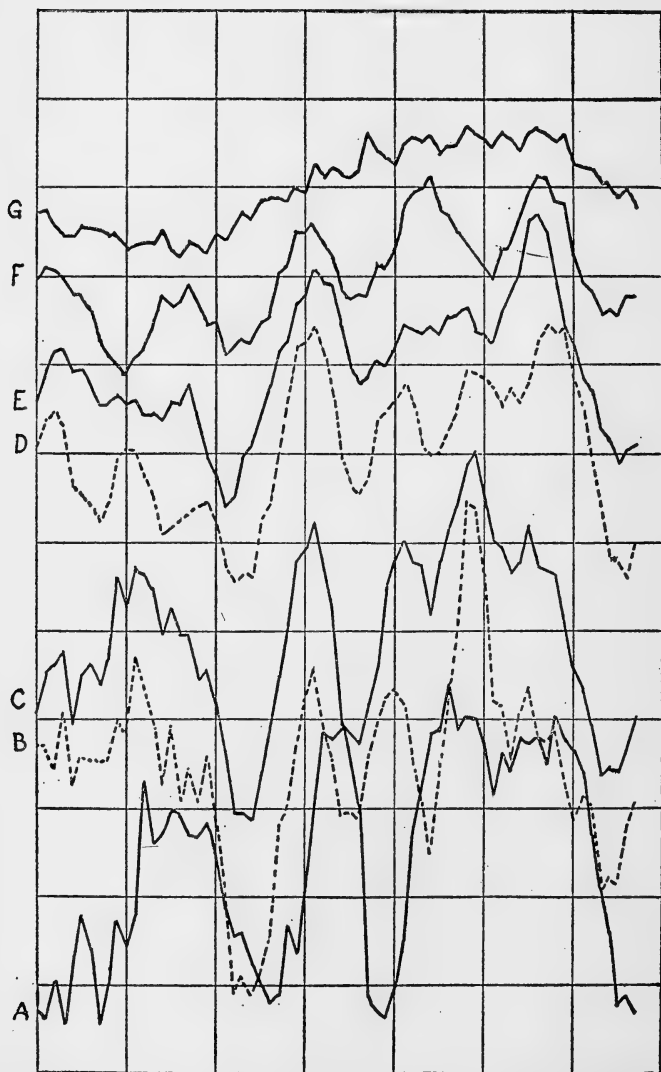


FIG. 25.—Precipitation, St. Louis, 684-month period, cleared of shorter harmonics. Three months shift of A. A and C observed before and after 1900 combined in B for further work.

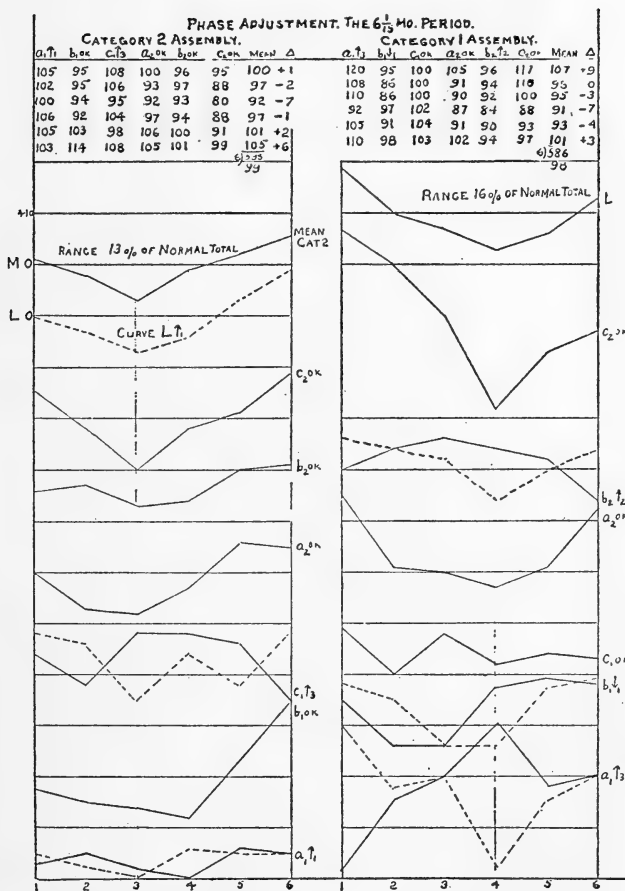


FIG. 26.—Phase adjustment for 6-column combination. Eastport, Maine, precipitation, $6\frac{1}{2}$ -month period.

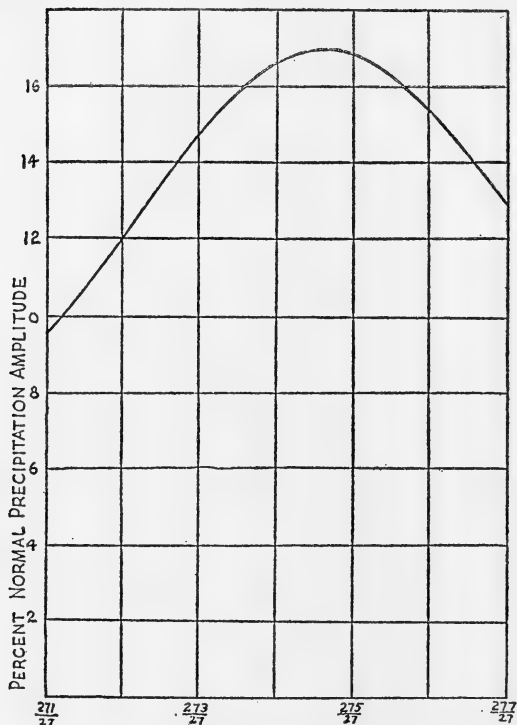


FIG. 27.—Exact length of the 273-month master period.

even more months, evidently for the same features. If these shifts could be predicted and corrected in advance, *very high* correlation coefficients would exist between predictions and events. As it is, correlation coefficients run from +50 to +70 percent at the different cities for precipitation, and from +30 to +50 percent for temperature reckoned from absolute zero.

9. ACCURACY OF PREDICTIONS

The average percentage difference between forecasts and events runs from 15 to 30 percent for monthly precipitation values at different cities. It runs from 1.5° to 2.7° F. monthly for temperature

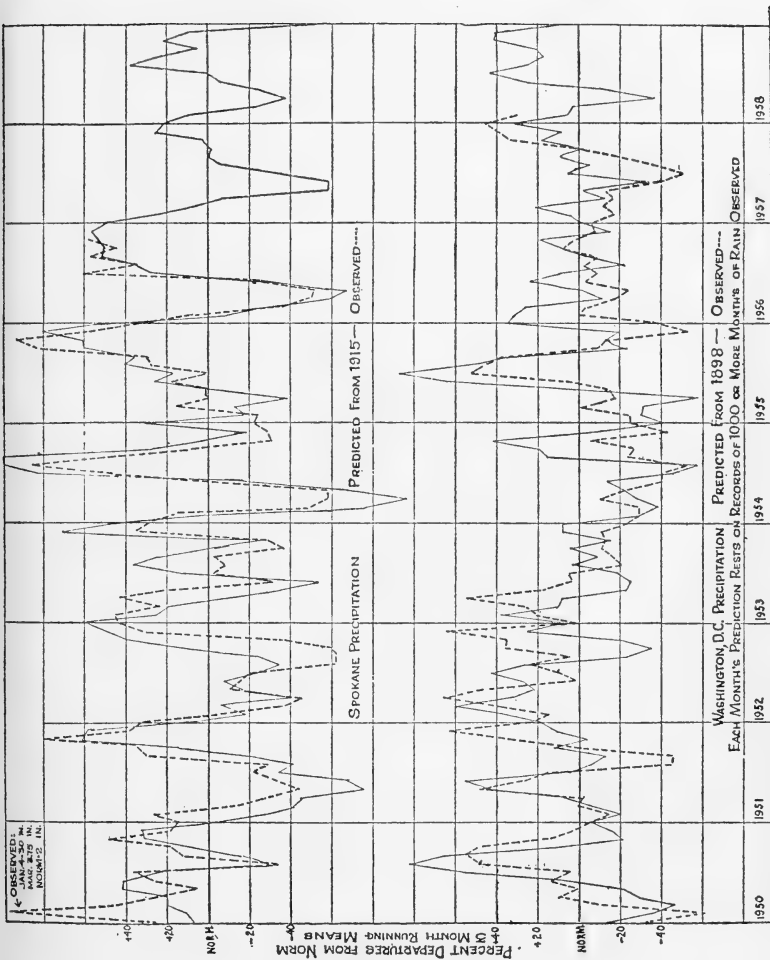


Fig. 28.—Forecast of precipitation, Washington, D.C., and Spokane, Wash., 1950 to 1958, compared with observed.

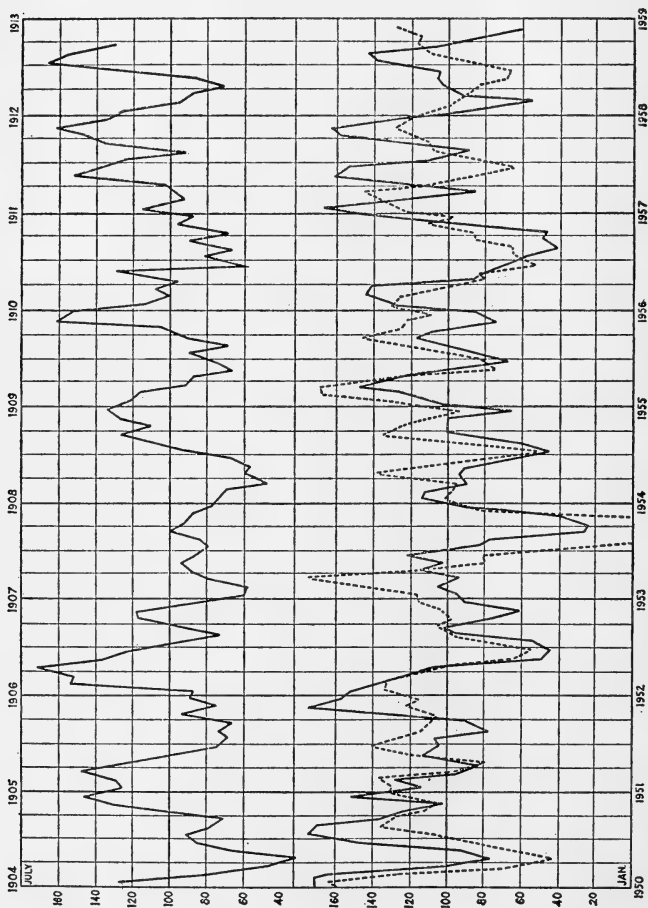


Fig. 29.—Forecast of precipitation, Nashville, Tenn., 1950 to 1958, and 1904 to 1912, compared to observed, 1950 to 1958

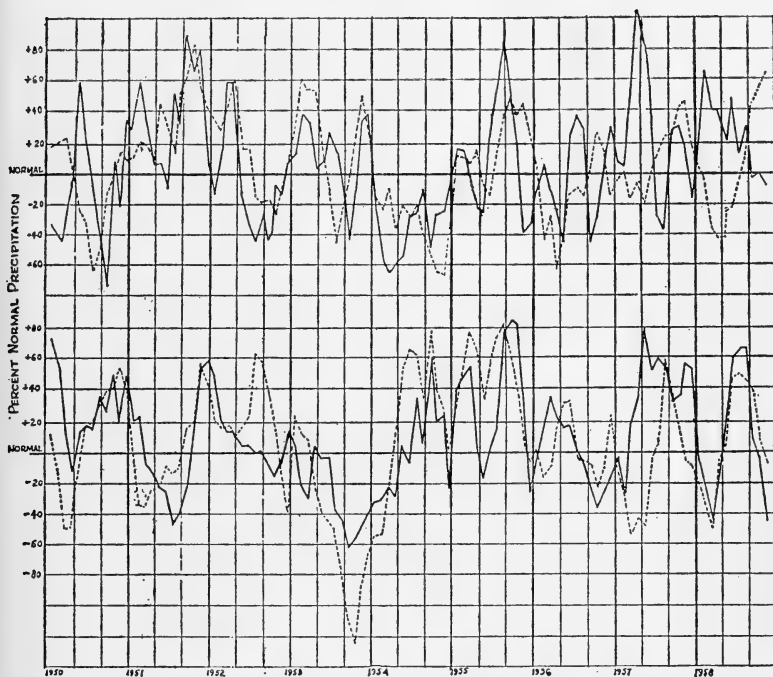


FIG. 30.—Forecasts of precipitation: Cincinnati, Ohio, below, Denver, Colo., above, 1950 to 1958, compared to observed.

forecasts. The shifts mentioned above heighten these average differences above what they would otherwise be. What most recommends the 10-year forecasts of precipitation is that they are about equally as accurate for times of wide departure from the normal as they are for times close to normal precipitation, as is shown for 14 cities in P. 4471, page 6 (here fig. 33).

10. MISCELLANEOUS MATTER RELATED TO SOLAR VARIATION

Ionospheric observations.—From measure of $h'F_2$ published by the Bureau of Standards, Mrs. Hill computed daily averages of $h'F_2$ from 1944 to 1957 (see P. 4338), for the hours 11, 12, 13. An earlier study had fixed the average monthly value for these

[Cont. p. 45]

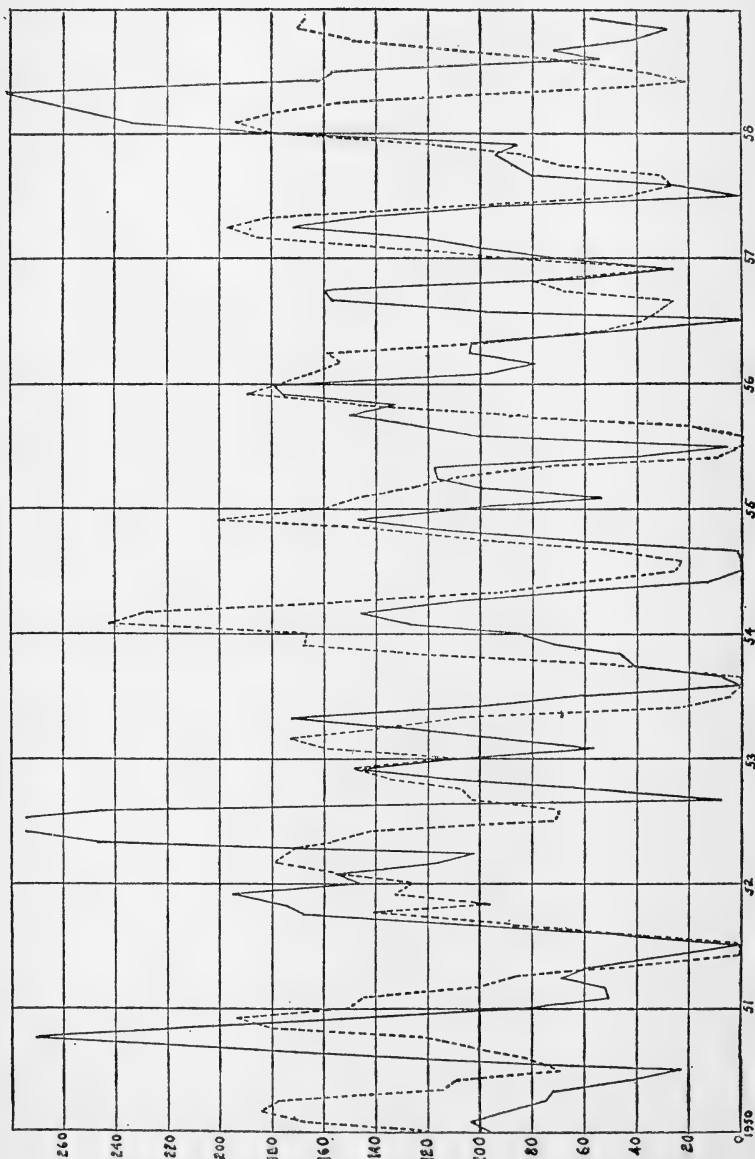


FIG. 31.—Forecast of precipitation, Sacramento, Calif., 1950 to 1958, compared to observed.

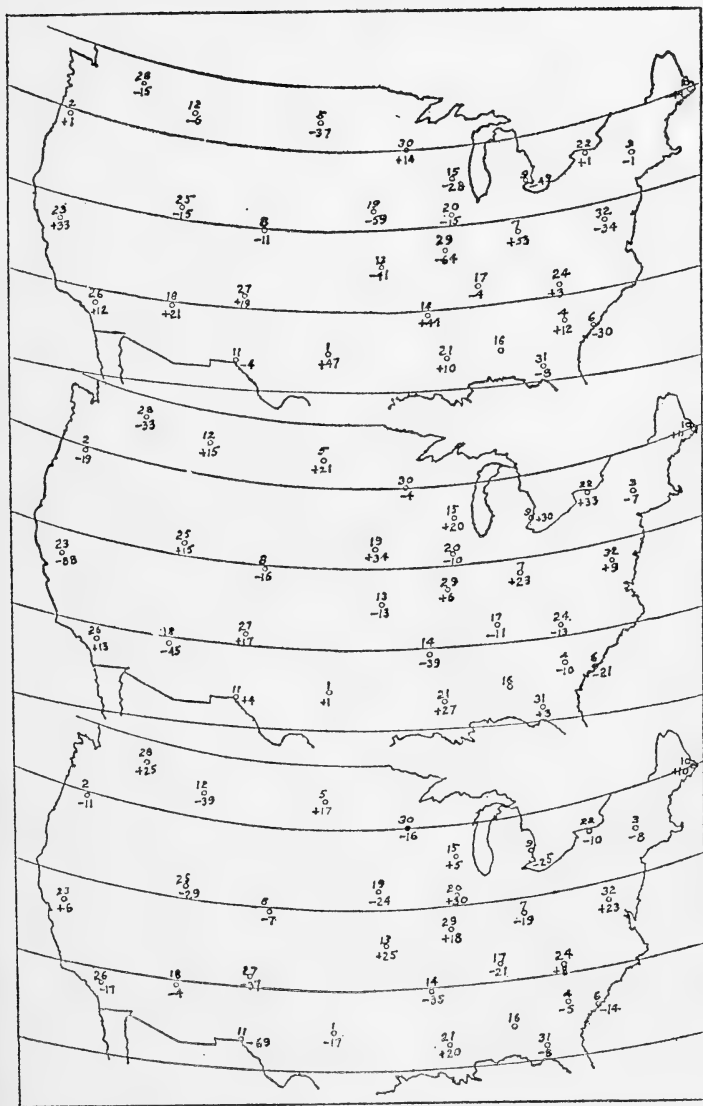


FIG. 32.—Map, forecast of precipitation, 32 stations, 1963, in 4-month means. Note: P. 4390 gives maps like this covering the years 1963 to 1967.

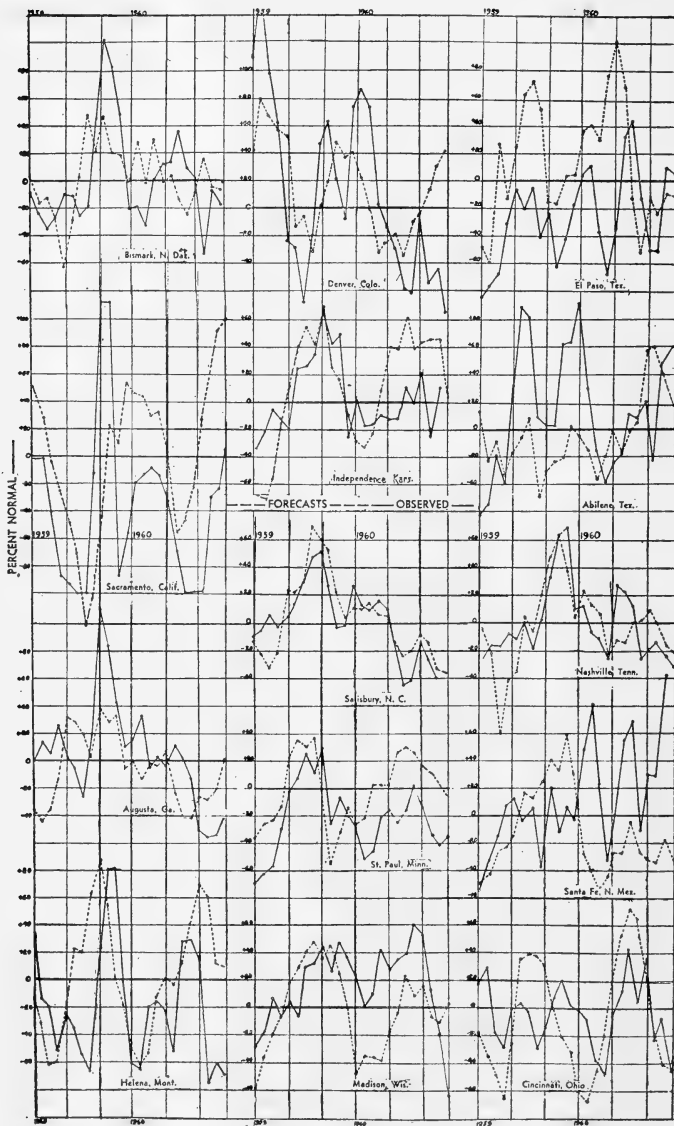


FIG. 33.—Verification of monthly forecasts of precipitation, 1959, 1960, for 14 stations.

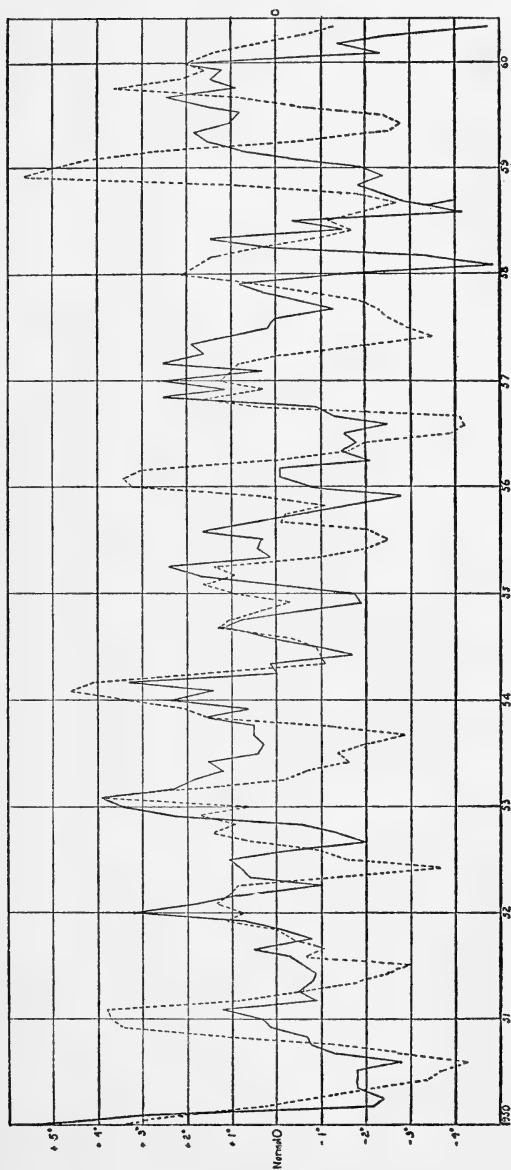


FIG. 34.—Forecast of temperature, Washington, D.C., 1950 to 1960, compared to observed.

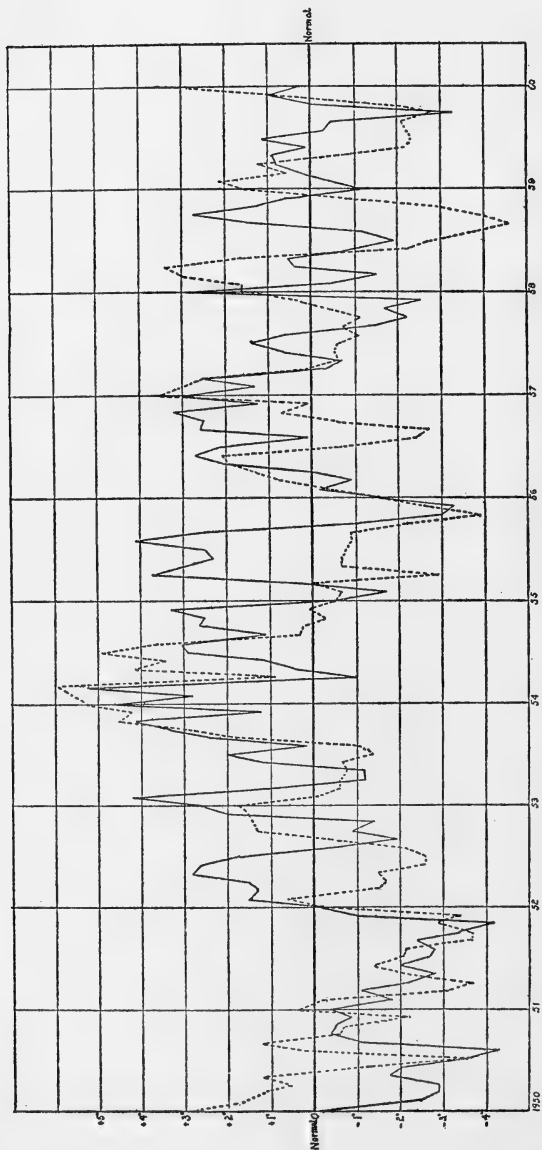


FIG. 35.—Forecast of temperature, Omaha, Nebr., 1950 to 1960, compared to observed.

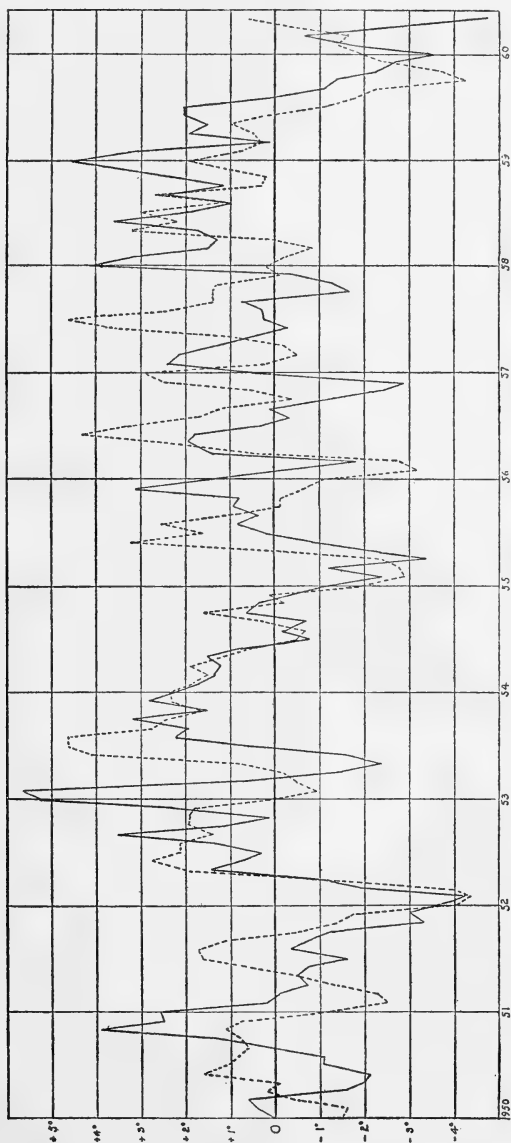


FIG. 36.—Forecast of temperature, Salt Lake City, Utah, 1950 to 1960, compared to observed.

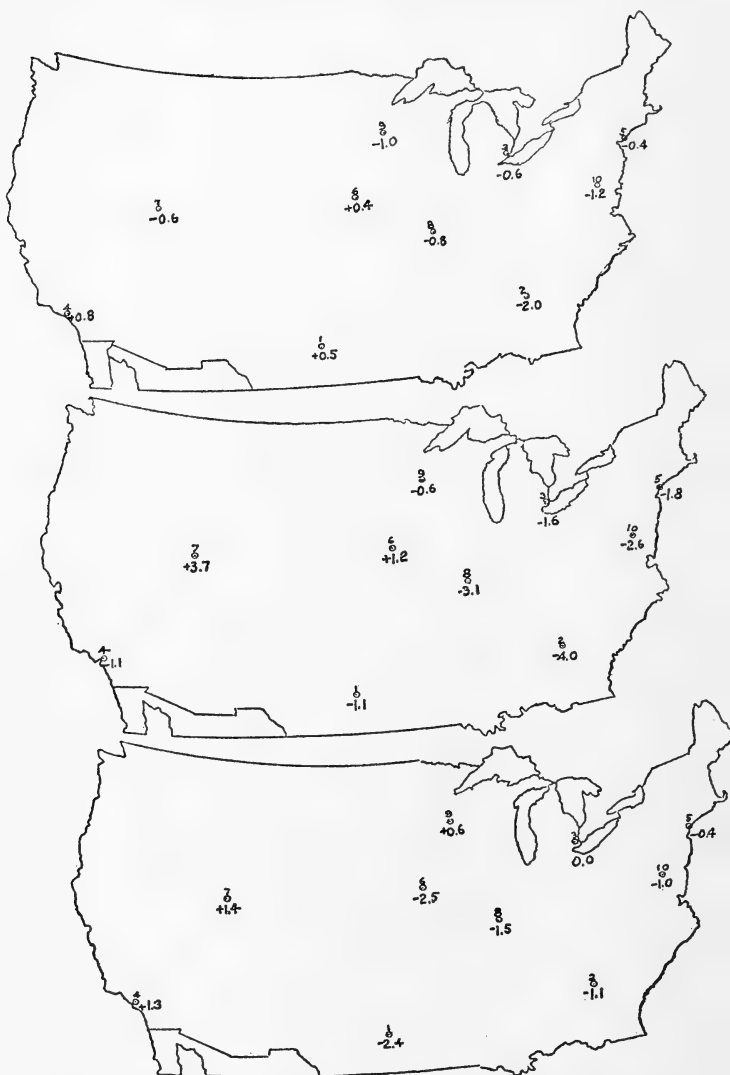


FIG. 37.—Map, forecast of temperature, 10 stations, 1963, 4-month means. Note: P. 4471 gives maps like this for the years 1963 to 1967.

hours at 315. Monthly means of Mrs. Hill's values were subtracted from 315 yielding the results given in table 6. (See fig. 39, p. 48.)

From these figures the average probable error of the monthly mean departures is ± 15 over the years 1944-1957. Combining the departures with observed mean monthly values of $h'F_2$, the observations are cleared of the yearly march and become adapted to show if they indicate relationship to the family of harmonics in solar variation. The result of this comparison is graphed in figure 39 and appears in table 7.

Within the limit set by the probable error, the graph shows sine forms for 7 of the 9 solar periods included. The other 2 are too short and irregular to judge.

Washington daily precipitation.—The sun's rotation period is approximately 27 days and is almost an exact submultiple of 2 years. The daily rainfall at Washington was tabulated from 1924 to 1941, 18 years, in 9 tables of 27 columns each. The 9 means of the 27 columns were then tabulated. This disclosed a small departure from exactly 27 days. The exact period of the solar rotation for the purpose in view was found to be 27.0074 days. P. 3765, figure 1, here reproduced as figure 40, shows how the rainfall of Washington was distributed over the period of the sun's rotation during the years 1924-1941. (See p. 49.)

The curve for years of average rainfall, No. 3, indicates that days 1, 2, 3, 4, 5, 12, 17, 22, 24, 25, 26, and 27 of the sun's rotation cycle (based on January 1, 1924) are apt to be more rainy than other days. From 1941 to 1954 I published yearly a pamphlet predicting 175 days of the next following year when precipitation was more likely to occur than on the other 190 (or 191) days. The experiment was successful beyond expectation. Indeed in 1948 no less than 14 brides wrote or phoned inquiring if their wedding day, to come in a month or six weeks, would be fair. I predicted 13 fair days and one probably rainy. As it turned out 14 were fair, but one was overcast without rain. The most outstanding success concerned the hostess in a restaurant. I told her that her day would probably be fair, but there would probably be rain the day before and the day after. That was exactly what happened!

TABLE 6.—Monthly mean departures of $h'F_2$ from 315.

Jan.	Feb.	Mar.	Apr.	May	June
−69±9	−27±14	−27±24	+29±30	+88±26	+89±25
July	Aug.	Sept.	Oct.	Nov.	Dec.
+93±19	+73±35	0±11	−52±13	−71±10	−73±9

TABLE 7.—Periodicities in monthly values of departures in $h'F_2$

Monthly periods	March of departures and probable errors								
2-23/24	+1.6	-2.5	+0.2						
	±1.1	±1.1	±1.1						
4-1/3	-5.4	+0.7	+0.1	+4.8					
	±1.5	±1.5	±1.5	±1.5					
5-1/18	-4.2	+2.6	+2.6	+1.5	+0.5				
	±1.6	±1.6	±1.5	±1.5	±1.5				
6-1/15	+6.9	+2.7	-2.7	-7.4	-2.2	-0.6			
	±1.8	±1.8	±1.8	±1.8	±1.8	±1.8			
7	-3.3	+1.1	+2.6	+3.4	-0.7	-3.3	-3.2		
	±2.0	±2.0	±2.0	±2.0	±2.0	±2.0	±2.0		
9-3/4	+2.1	-2.9	-4.2	-5.0	-2.2	+4.6	-1.4	-4.4	
	±2.1	±2.1	±2.1	±2.1	±2.1	±2.1	±2.1	±2.1	
	+3.9	+1.0	
	±2.1	±2.1	
10-1/9	-8.5	-7.2	-4.1	-1.7	+1.6	+2.4	+8.5	+7.2	
	±2.1	±2.1	±2.1	±2.1	±2.1	±2.1	±2.1	±2.1	
	-0.5	-3.9	
	±2.1	±2.1	
11-3/8	+4.2	+7.9	+7.8	+0.5	+0.1	-10.0	-4.9	-4.3	
	±2.2	±2.2	±2.2	±2.2	±2.2	±2.2	±2.2	±2.2	
	-5.1	-2.8	-0.7	
	±2.2	±2.2	±2.2	
15-1/6	-3.4	+8.3	+6.0	+7.1	+5.1	-1.4	-2.5	+0.2	
	±2.3	±2.3	±2.3	±2.3	±2.3	±2.3	±2.3	±2.3	
	-3.1	-1.7	-5.3	-7.3	-8.7	-4.7	-0.3	..	
	±2.3	±2.3	±2.3	±2.3	±2.3	±2.3	±2.3	..	

The following table 8 shows the results from 1934 to 1954. I give the ratios of yearly rainfall which came on 175 preferred days to that which came all other days. The expected ratio is 1.42.

In the year 1952 a peak rainfall 6 times the average of all other days of the cycle appeared on the eleventh day. In 1953 the peak had fallen to 3 times but was still extraordinary. I have wondered if the surprise was caused by atomic bombing. After 1954 I was too immersed in long-range forecasts, solar boilers, and my second marriage to continue with Washington daily rainfall.

Various periods.—

1. The 6.6485-day period.

TABLE 8.—Precipitation of Washington.
Ratio 175 preferred to 190 (191) other days

Years ..	1934-1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	Mean Ratio 1.45
Ratio ...	1.55	1.48	1.06	1.45	1.10	1.28	1.56	1.49	1.34	—	—	1.31	

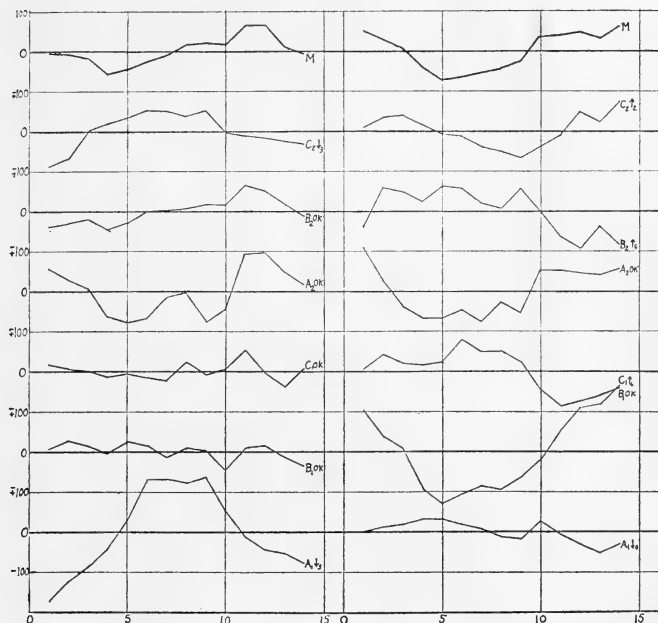


FIG. 38.—Phase adjustments for 6-column combinations, Washington D.C., temperature, 13% month period.

Many have noticed that if a rain comes Saturday it may recur on several succeeding Saturdays and after that on Fridays. We have tabulated daily temperature in New York and Washington to investigate this observation. We discovered a well-marked period (fig. 41) of 6.6456 days (later improved to 6.6485 days) and also the half of it in the weather of New York and Washington. (See also P. 2499, P. 3893, P. 3990, and P. 4015.) The period was found to be within 1 percent or less of $1/1250$ of 273 months as computed employing the exact period of the earth's revolution about the sun. The shorter period is exactly $273/2500$ months.

2. Human pulse periods.

My friend Dr. Frances P. Marshall has a 3-year daily record of her pulse taken before rising each morning. She permits me to publish my analysis of it (see P. 4265, pp. 15-17). A very smooth

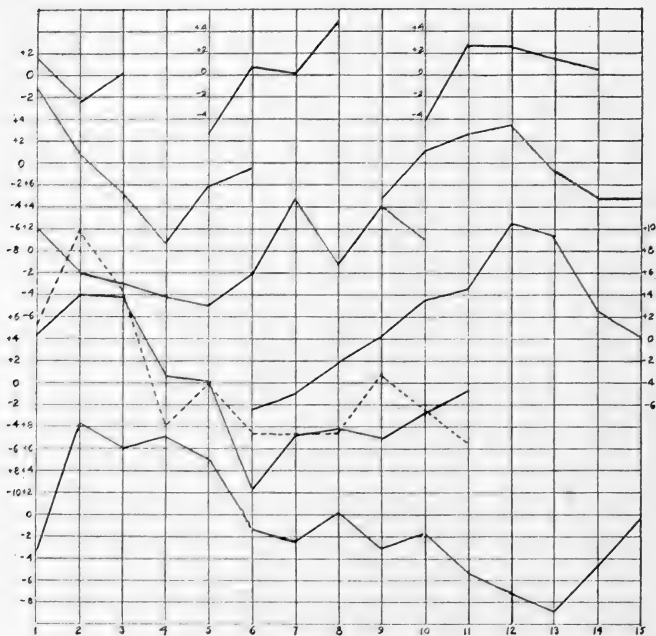


FIG. 39.—Periods in ionospheric $h' F_2$, harmonics of 273 months.

sine curve of 7.0 months, shown in figure 42, was found after clearing the original 7 months observations of harmonics of $1/2$, $1/3$, $1/6$, $1/7$, $1/11$ of 212 days. Its amplitude is 2 pulses on 67. All the periods named are of course exact submultiples of 273 months (p. 51).

3. Droughts at long periods.

By invitation I published in the year 1938 an article on solar variation and weather in *Zvláštní Otisk*, the organ of the physicists at Prague in Czechoslovakia. In that article, so far as I can discover now, appeared my first prediction of very long-range solar periods. I quote: "Records have been kept of the levels of the Great Lakes of North America regularly since 1860. In addition, partial records exist which fairly indicate the levels of some of the lakes since 1837. From these sources I have prepared figure 6 [here fig. 43, p. 52] which indicates the water-gauge values for Lake Huron for a cen-

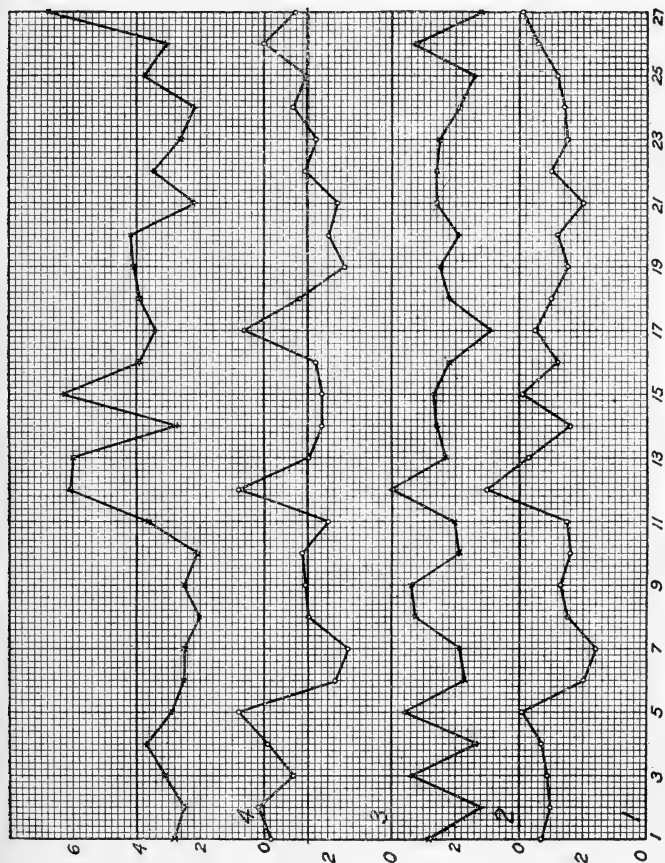


FIG. 40.—Period of 27.0074 days in Washington precipitation. See P. 3765.

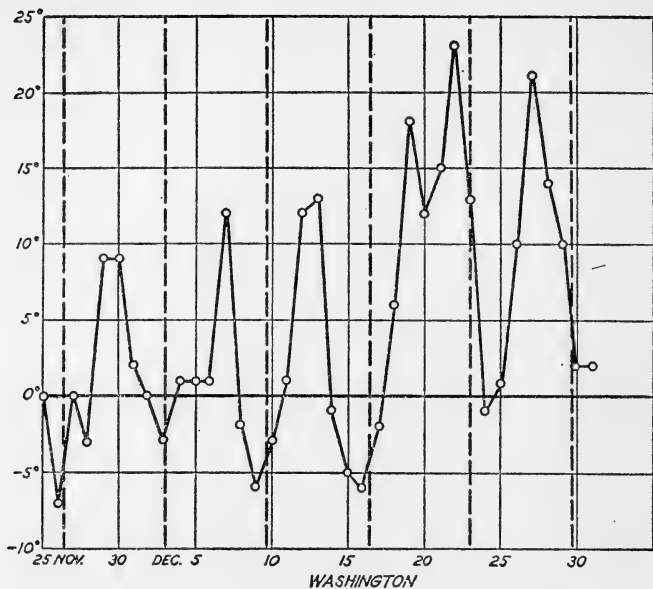


FIG. 41a.—Period of 6.6485 days in Washington, D.C., weather.

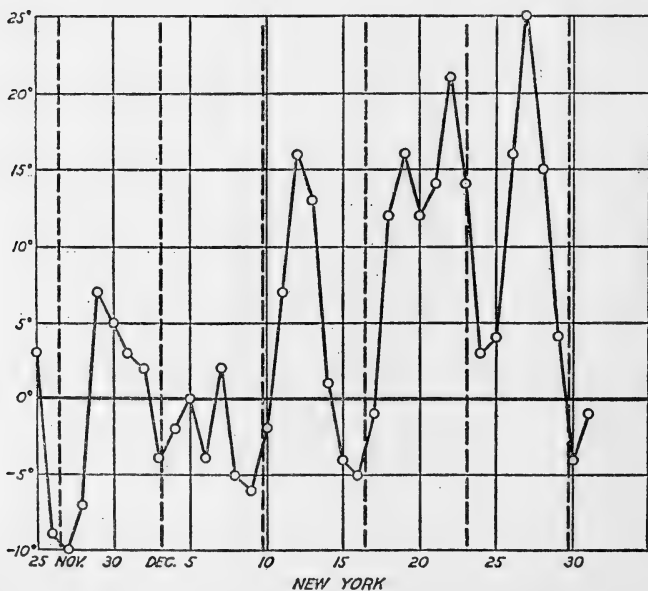


FIG. 41b.—Period of 6.6485 days in New York City weather.

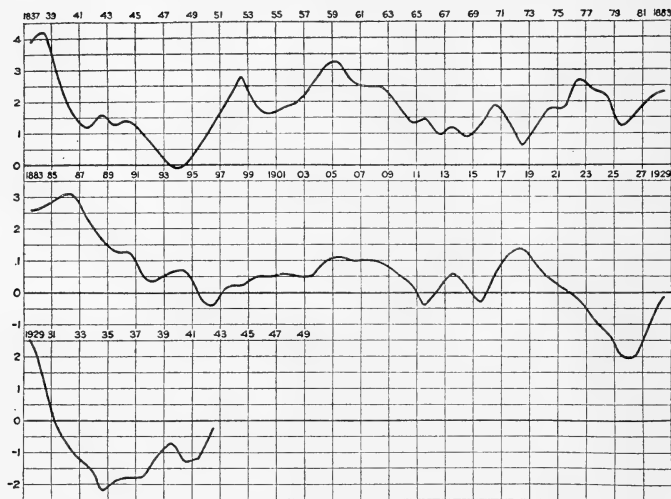


FIG. 43.—Periods in level of Lake Huron.

fig. 6). The two great droughts will probably begin about 1975 and 2020, respectively.

11. SHORT ACCIDENTAL TRENDS IN SOLAR VARIATION

Measurements of the solar constant of radiation reveal trends of rising and of falling radiation several times each month lasting from 3 to 10 days each (see fig. 45). We noticed as early as 1925 that the temperature at Washington seemed to respond to these accidental solar changes. This led us to make a very extensive investigation of this matter, in which we found (P. 3771, P. 3893, P. 4462) that not only the measures of the solar constant of radiation but also measures of the areas of solar flocculi and measures of Fe in the ionosphere precede up-and-down temperature trends. These trends, observed either in solar constant, calcium flocculi, or Fe changes, produce opposite effects, like the right and left hands, on temperatures the world over. (See figs. 45, 46, and 47.) The temperature changes are not small. I cannot better bring out this phenomenon than by quoting from pages 219-221 of my paper of 1939 (Quarterly Journal Royal Meteorological Society, vol. 65, No. 280, April 1939).

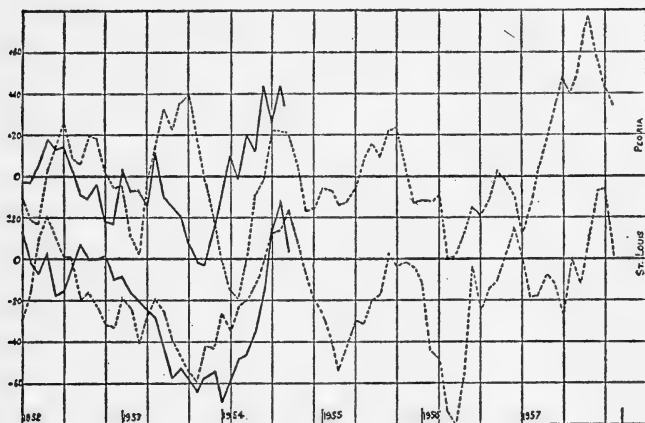


FIG. 44.—Drought prediction from forecasts of precipitation, St. Louis, Mo., and Peoria, Ill.

Referring to Fig. 1 of my just cited paper, here reproduced [here figure 46], the reader will find there two curves for each month of the year showing departures from normal temperature at Washington, D.C. In each month the curves show a well-marked opposition like the right and left hands. The separations of the curves in the months January, February, March, April, May, June, August, October, November, and December range from 14° to 24° F., and evidently constitute major departures from normal temperatures. Similar results, showing in almost all cases opposition like the right and left hands, but differing widely in actual march of the pairs of curves, are shown for St. Louis, Helena, and Potsdam, in other illustrations in the cited publications. The curves are computed for all these cities starting from identical dates, 320 in number, scattered over 12 years. Some 10 to 20 cases combined are in each curve shown. The data of temperature departures in each case cover 16 days following the starting date selected.

How were these 320 dates selected? They are chosen as dates when solar variations commenced. As shown in Fig. 1 and Table I of "The dependence of terrestrial temperatures on the variations of the sun's radiation," they comprise all the dates during 12 years when good consecutive solar constant observations, made mostly at Montezuma, Chile, began to indicate rising or falling sequences of the sun's output of radiation. The range of these sequences was small, rarely exceeding 1 percent, and their mean range is only about 0.7 per cent of the solar constant. Owing to the interference caused by changes in atmospheric transparency, superposed on the inevitable accidental errors of measurement, it is highly probable that some of these 320 cases are spurious. If the spurious cases could be eliminated the average temperature departures would doubtless be increased above their already large magnitudes.

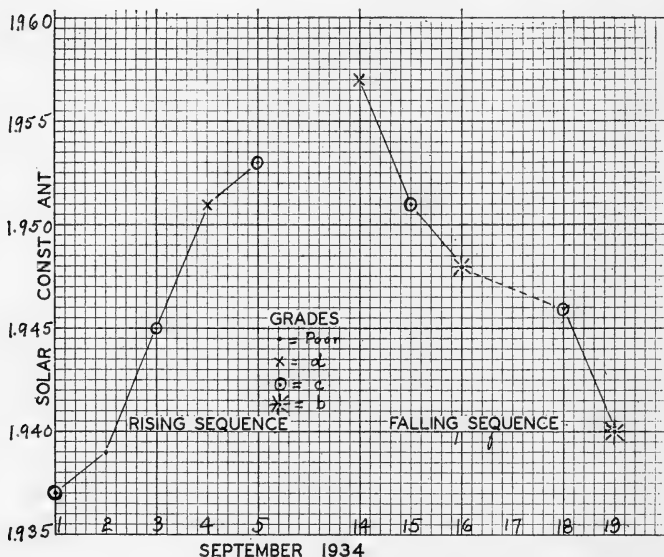


FIG. 45.—Solar constant, rising and falling trends.

Our critics, however, maintain that they have demonstrated by correlation methods, and by references to my writings, that the supposed variation of the sun is largely due to defects in our methods of observing, and that the consequences deduced from such supposed variations are illusory.

If so, we must assume that these interesting curves, which show such extraordinary inversions of temperature departures, would as likely as not result from a haphazard choice of any 320 dates, quite as well as from the selection of 320 dates which were chosen because they were observed to be the dates of commencing solar changes. This is of course absurd.

Several of my friends have urged me to omit the just-preceding part of my defense. They consider that meteorologists are so firmly fixed in their disbelief in the meteorological importance of day-to-day solar variations that no meteorological evidence whatever can persuade them to reconsider the matter. But though I may be singular in my opinion, I regard the present argument as unanswerable. Though it may be futile for the present, owing to this prevailing attitude, I shall proceed to place on record still more support of my argument.

First, as I showed in my paper, "The dependence of terrestrial temperatures on the variations of the sun's radiation," above cited, not only do several cities show large opposing trends of temperature following rising and falling sequences

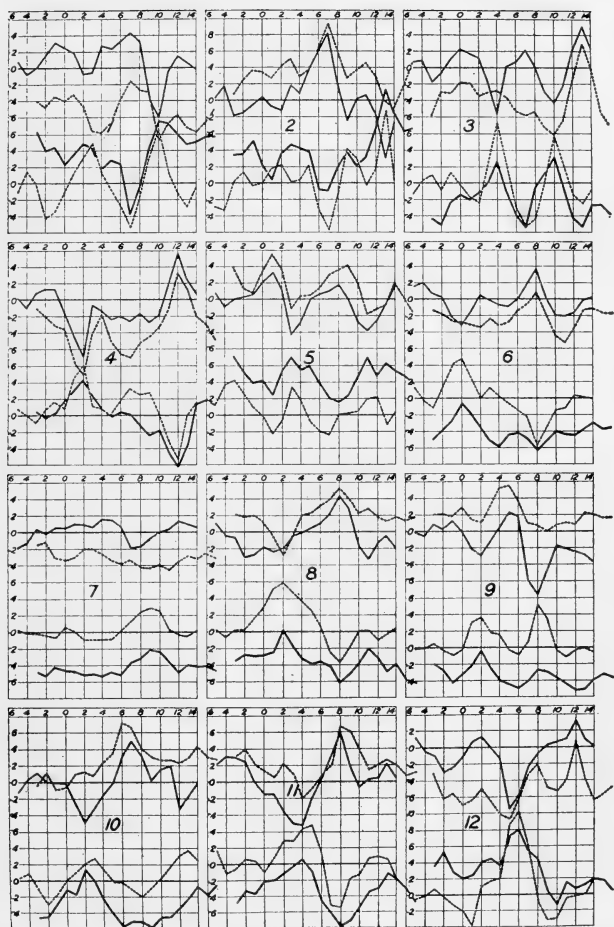


FIG. 46.—Temperature, Washington, D.C. Opposed effects follow rise and fall of solar constant and, 2 days later, of calcium flocculi observations, January to December.

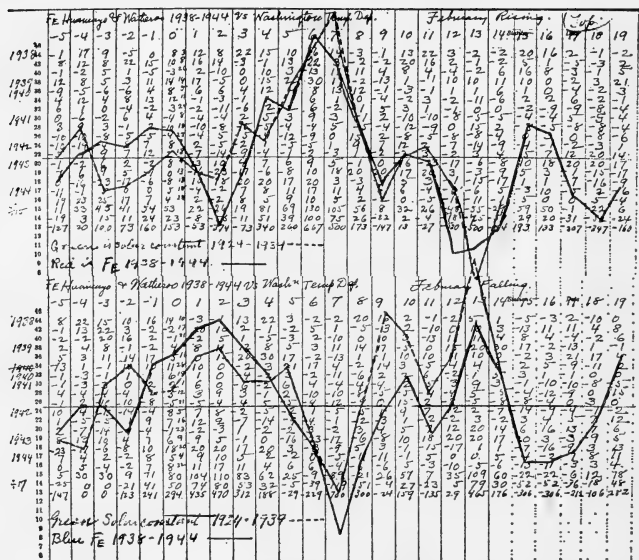


FIG. 47.—Temperature, Washington, D.C. Opposed effects follow rise and fall of solar-constant and ionospheric observations.

of observed solar variation, but 46 cases of unusually great observed solar changes were followed on the average by 1.95 times as large temperature changes in the same phases as the mean of 150 cases of all amplitudes. Again, the average trends of temperature following solar changes, as observed in the years 1924 to 1930, were nearly identical in phase, magnitude and form with those observed in the years 1931 to 1935.

But now I offer a new evidence which I think is even more convincing. If, in reality, the observed variations of the sun were real, and influenced temperatures greatly for 16 days after their incidence, there still seems no reason to think there should have been any unusual temperature effects immediately before their occurrence. I have therefore computed for each of the 320 dates the march of temperature departures from normal for 16 days preceding the dates in question. I have then computed correlation coefficients for Washington as between the average marches of temperature attending rising and falling solar sequences, both after and before the beginnings of the sequences of solar change.

To fix ideas, I recall that in each division of this test there are 24 lines comprising 17 values each, two lines for each month of the year, selected from the 12 years, 1924 to 1935. These pairs of 24 lines of the divisions are separated into two types, one type containing 17 values for days following,

and 17 for days preceding the beginning of sequences of observed *rising* solar radiation. The other type comprises 17 values for days following and 17 values for days preceding the beginning of sequences of observed *falling* solar radiation. Two correlation coefficients are to be computed, one including the 204 values of the two contrasted types *following* the supposed critical dates, the other for the 204 values of the two types *preceding* them.

In order to avoid diluting the correlations by including extraneous influences due to previous conditions, each line was first reduced to the level of zero temperature departure, by adding to all 17 values in that line a constant quantity such as to make the average temperature departure for that line zero.

Having thus arranged the values, correlation coefficients were computed between the two types for the two divisions. They resulted as follows:

After appearance of solar change, $r = -54.3 \pm 4.9$ per cent, which is significant.

Before appearance of solar change, $r = 11.1 \pm 6.0$ per cent, which is meaningless.

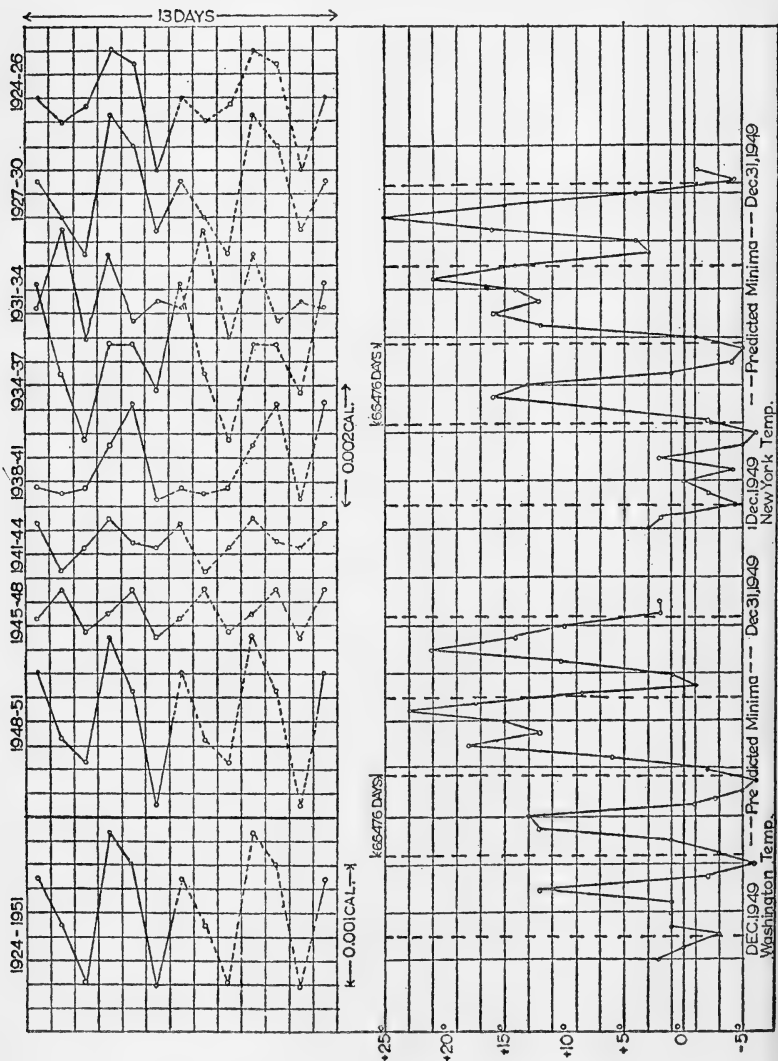
The inference is obvious that the 320 dates, above described, were dates of real significance, since no other consideration was used in selecting them, and it is difficult to avoid the conclusion that they were dates when real solar changes began.

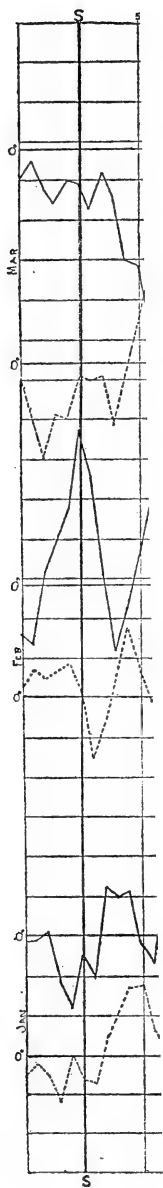
In what follows I shall show that the ionospheric Fe and the areas of calcium flocculi are both as effective as are solar constants for this observation. (See figs. 45, 46, 47.)

Graphs from other publications will show plainly how important this matter is. My latest paper on the subject, P. 4462 (see figs. 48, 49), shows how a modern satellite could obtain first-rate solar constant values daily, and the results radioed to earth would give means to predict temperature changes all over the world for 16 days in advance. Furthermore, if such satellite continued indefinitely to circle the earth we would have means to discover great changes in the solar radiation like that of 1922 and 1923 if they occur. This might lead in course of a century or more to discovery of long-period variations of solar radiation of high importance.

12. DRIFT OBSERVATIONS

As stated in the introduction, and illustrated in plate 1, our Mount Wilson observing station was equipped with a tower telescope. The solar image, about 8 inches in diameter, fell upon the slit of the spectrobolometer in such a way that when the telescope clock was stopped the solar image drifted centrally over the slit. The spectrobolometer was set for any desired wavelength, and the intensity of that wavelength along the sun's central diameter was recorded as the solar image drifted. In 1908 we began to make these drift records





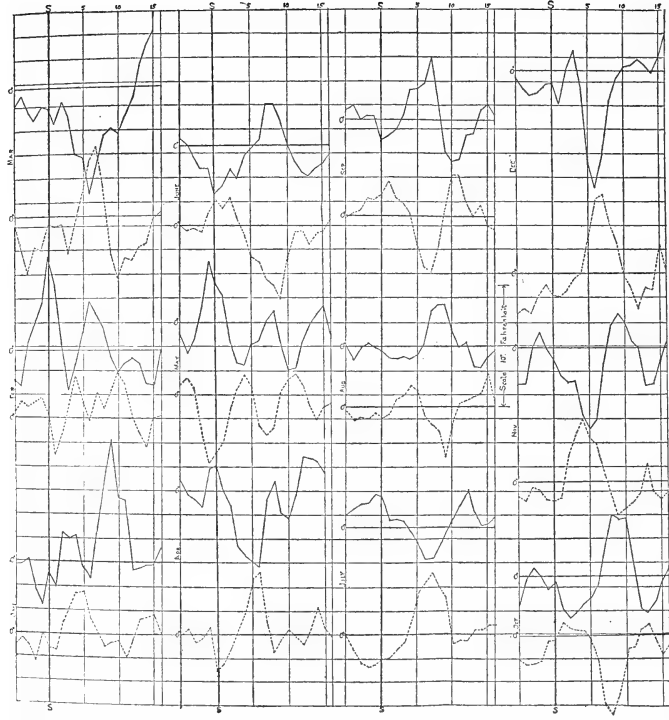


FIG. 49.—Washington temperature controlled 16 days by sun's variation. The sun changes at S. Washington temperature, —5 to 16 days. Full curves, solar radiation rises, falls. Dotted curves, Zero departures at O. See P. 4462.



every time bolographs of the solar spectrum were made for measuring the solar constant of radiation. This continued until 1920, when we removed from regular observation on Mount Wilson.

Our purpose was to determine if changes in the solar constant are accompanied by correlated changes in the U-shaped drift curves. Dr. Langley had hoped that they would be and that drift observations would serve as an easy means to measure solar variation.

The entire series of comparisons between solar-constant variation and solar-contrast variation is studied in chapter 7 of A.P.O. Annals, volume 4, pages 217-258. The discussion of this long series of careful measures gave conflicting results, hard to understand. Sometimes it indicated increased solar constant with increase of contrast in brightness between center and limb of the sun. Indeed, for the results of 1913, the correlation coefficient was $+0.601 \pm 0.067$, and a change of 1 percent increase of the solar constant was accompanied by +17 in the arbitrary solar-constant number. But at some times even the sign of the correlation coefficient changed from plus to minus. So the hope that Dr. Langley had held before his death in 1906 proved illusory. Solar-contrast observations did not yield an easy way to measure the variation of solar radiation.

In May 1952, however, P. 4088 threw new light on this difficulty. We then knew of the family of harmonic periods in solar variation. Synthetic solar constant values computed from these periodic terms marched in close accord with observed values from 1920 to 1951 (P. 3902). So good was this agreement that I computed the probable march of the solar constant from 1900 to 1920, the years before good determinations had been possible. For, as I have said, the Langley solar-constant method, though sound and fundamental, must always give values too high or too low if the transparency of the atmosphere changes during the several hours required to measure it. The synthetic solar-constant values (see fig. 50) were based on "the short method" which has no such drawback, and besides gives several values of the solar constant on each day of observation, thus providing mean values. (See pp. 61, 62).

Figure 50 shows that before 1920 there is no visible correlation between the observed and the synthetic Mount Wilson solar constant values. But figure 51, in its graphic comparison of synthetic solar constant with observed solar-contrast values, shows a fairly high degree of correlation. Increased contrast goes with increased solar constants. So if the A.P.O. was still in short-method operation as

formerly, and in a good location, and with a tower telescope, perhaps Dr. Langley's hope might be at least partly realized.

13. FINAL EVIDENCE

Notwithstanding the evidences contained in the references cited below some meteorologists may still be reluctant to accept forecasts many years in advance. In the absence of conclusive *theoretical* demonstration that the small percentage changes in solar radiation can cause changes of identical periods of many times larger percentage in weather, and that these are hidden by phase changes from direct disclosure, they may still withhold belief. Therefore I present an additional observation which is so striking that some have considered it conclusive.

If it is true that the 273-month family of regular harmonic periods exists in weather, with such amplitudes that by their summation a controlling influence is exerted, then it follows that the weather should tend strongly to repeat its features at intervals of 22 years 9 months. I showed such a tendency in the precipitation of Peoria, Ill., in 1934 by figure 33 of P. 3339, reproduced as figure 1 of P. 4095, 1952. But now I will present a much more telling evidence from the records of precipitation at Nashville, Tenn.

Taking from our files the computations on Nashville prepared for P. 4390 in 1958, I lengthened my forecast for Nashville through 1970. Considering only the 6 years 1965 through 1970, I looked back 22 years and 9 months to the interval April 1942 to March 1948, 6 years.

Figure 53 gives a graphical comparison of my *forecast*, from 1965 through 1970, with the *observed* precipitation at Nashville from April 1942 through March 1948. The values plotted are, as stated in P. 4390, smoothed by 3-month consecutive means and are departures from the normals given in table 9, P. 4390. I have computed the correlation coefficient for the 6 years between the two curves of figure 53, and also the correlation between the two curves of figure 2, page 3, of P. 4390, for the 6 years 1950 through 1955, all from Nashville precipitation. The two correlation coefficients are, respectively, $+0.469 \pm 0.061$, and $+0.737 \pm 0.024$.

So the correlation coefficient between the *direct forecast* and the *event*, 1950 through 1955, is 30 times its probable error, and the correlation coefficient between the *forecast*, 1965 through 1970, and the *observed* precipitation at Nashville, April 1942 through March 1948 (22 years 9 months previous) is 7.6 times its probable error.

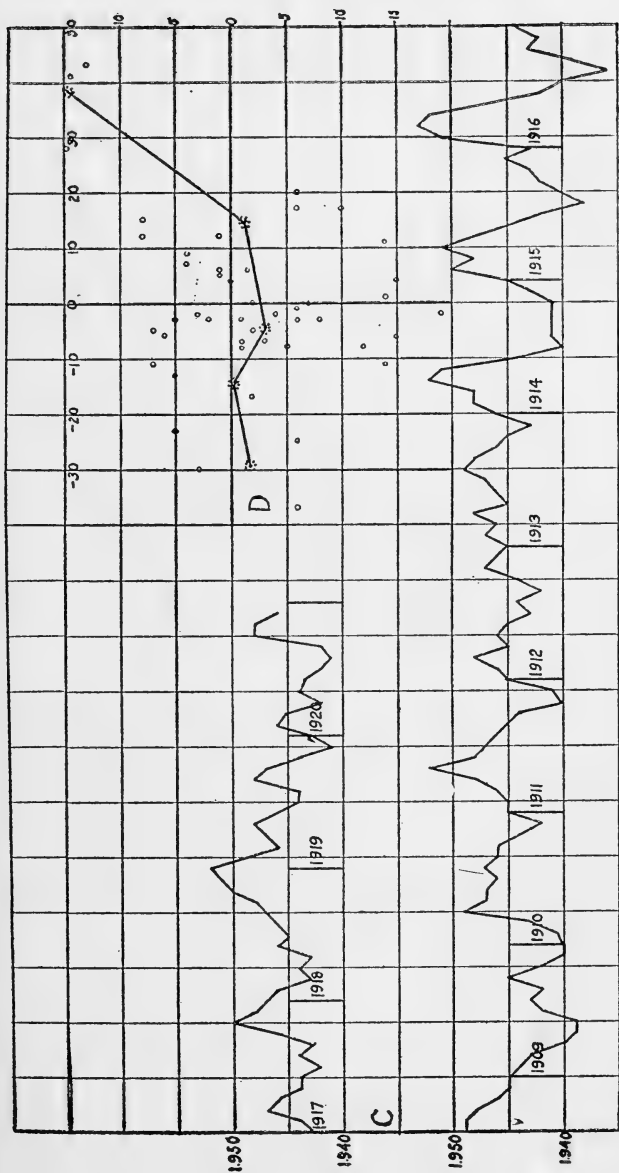


FIG. 50.—Solar constant backcasted, 1920 to 1909, No correlation with Mount Wilson observed.

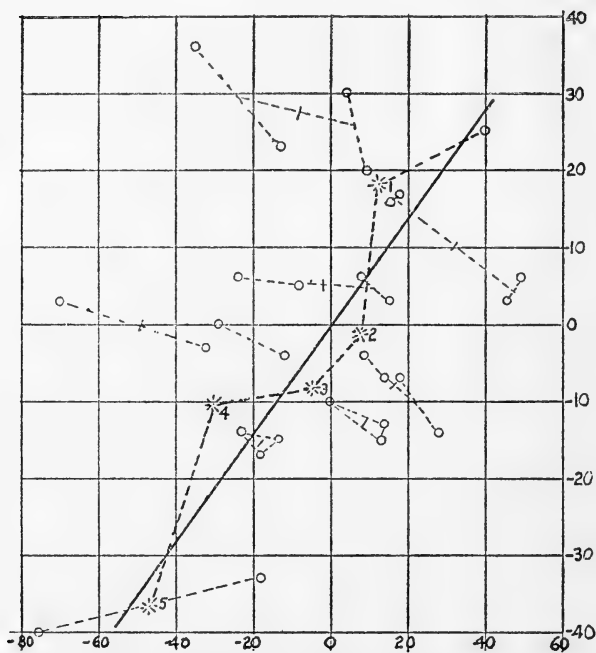


FIG. 51.—Solar constant (backcasted) versus solar contrast, 1913 to 1920.

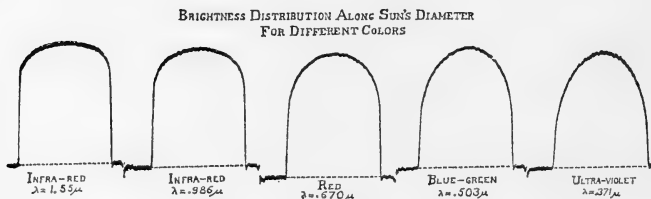


FIG. 52.—Solar contrast, center to solar limb, observed, 5 wavelengths.

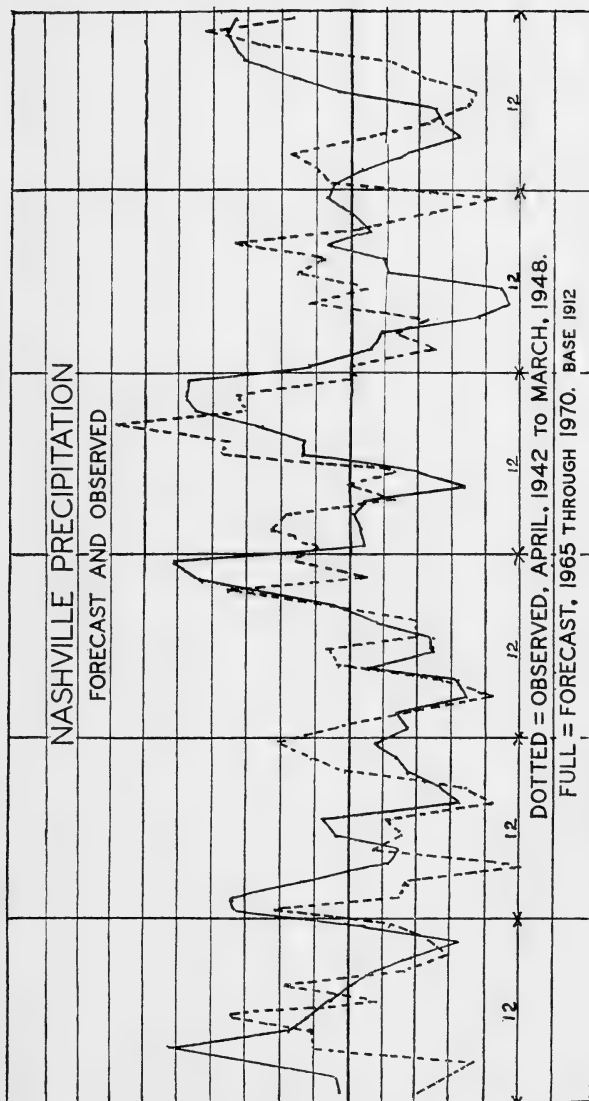


FIG. 53.—Nashville precipitation: Forecast, 1965 to 1970, versus observed, 1942 to 1948, 273 months previous.

Considering probable changes of an accidental character that may have happened in the long interval of 22 years 9 months, I do not think a fair-minded critic should object because the latter coefficient is smaller than the former. For, after all, the correlation coefficient for the interval 1942-1948 is almost 50 percent and nearly 8 times its probable error.

CONCLUDING REMARK

In the present paper I have summarized 13 aspects of the dependence of weather on solar variation. But without unduly expanding the paper, I could not give half of the evidence that supports these positions. My best course is to give in the Appendix references to many papers where, by tables, illustrations, and text, the evidence is amplified for those who may be interested. I would like to call attention particularly to Publications 4088, 4090, 4103, 4135, 4211, 4213, 4222, 4352, 4390, 4462, and 4471, where much that I have not crowded into this paper will be found. I have suggested there one theoretical hint as to the nature of the connection between solar variation and weather (P. 4211, pp. 10-11). Also the atmospheric conditions that prevent discovery of the family of regular periods in weather by *cursory* tabulations are more fully explained. I am still hopeful that meteorologists in America will at length see that a useful measure of long-range forecasting, even to a half century in advance, can be attained by using the records of the past with due attention to atmospheric conditions.

APPENDIX

REFERENCES TO THE ORIGINAL INVESTIGATIONS SUPPORTING STATEMENTS IN THE TEXT

(The boldface numerals refer to the numbered sections of the text)

<i>Publ. No.</i>	<i>Date</i>	<i>Reference</i>	<i>Subject</i>
	1908	Ann. A.P.O., vol. 2, pp. 13-17.....	1 Theory of Langley method for solar constant.
	1913	{ Ann. A.P.O., vol. 3, pp. 21-39.....	1 Complete procedure for solar constant, Langley method.
		{ pp. 47-52.....	1 Silver-disk pyrheliometer.
		{ pp. 52-69.....	1 Water-flow and water-stir standard pyrheliometers.
		{ p. 158.....	1 Radiation and wavelength, solar diameter distribution.
	1915	{ Smithsonian Misc. Coll., vol. 65, No. 4.....	2 Solar constant observed Sept. 20 and 21 from sunrise to noon.
		{ Do	All 6 values obtained by Langley method. All 1.90 to 1.96.
2361		{ Do	2 Balloon pyrheliometer flown July 11 records value of 1.87 calories at 2.63 mm. pressure.
		{ Do	2 Curve of highest values, sea level to highest balloon, gives solar constant of 1.93 calories.
2499	1918	Smithsonian Misc. Coll., vol. 66, No. 6	Solar rotation and solar variation. Periods 27 days and $\frac{273}{1250}$ months shown by correlation in 1915 and 1916.
	1922	{ Ann. A.P.O., vol. 4, pp. 65-84.....	2 Pyranometer; brightness of sky; solar disk.
		{ p. 219.....	12 Drift curves, 5 wavelengths; solar disk.
		{ p. 250.....	12 Drift curves and haze.
		{ pp. 217-257.....	12 Solar constant and solar contrast.
3182	1932	Smithsonian Misc. Coll., vol. 87, No. 15.....	1 Improved water-flow pyrheliometer and its standard scale of solar radiation.
1938		Zvláštní Otisk XVIII, Prague.....	10 Some periodicities in solar physics and terrestrial meteorology; droughts predicted from Great Lakes level records.

APPENDIX—continued

<i>Publ. No.</i>	<i>Date</i>	<i>Reference</i>	<i>Subject</i>
	1942	{ Ann. A.P.O., vol. 6, pp. 83-162..... p. 163.....	Solar-constant measurements. Station values compared for accuracy.
3765	1944	Smithsonian Misc. Coll., vol. 104, No. 3.....	A 27-day period in Washington precipitation.
3771	1944	Smithsonian Misc. Coll., vol. 104, No. 5.....	Weather predetermined by solar variation.
3893	1947	Smithsonian Misc. Coll., vol. 107, No. 4.....	Sun's short period. $6.6456 \text{ days} = \frac{1}{1250} \times 273 \text{ months}$.
			Also sun's radiation has irregular trends up and down, which produce opposite marches of temperature for 2 weeks thereafter. These trends occur also in ionospheric Fe and in areas of calcium flocculi near central sun.
3916	1948	Smithsonian Misc. Coll., vol. 110, No. 1.....	Solar variation attending West Indian hurricanes.
3940	1948	Smithsonian Misc. Coll., vol. 110, No. 6, fig. 1 (see also fig. 4 and pls.)	Solar variation attending magnetic storms; effects of great sun-spot group, Mar. 20, 1920.
3990	1949	Smithsonian Misc. Coll., vol. 111, No. 13.....	Washington and New York respond equally to temperature influence of the 6.6456-day solar period.
4015	1950	Smithsonian Misc. Coll., vol. 111, No. 17.....	Predictions of Washington and New York minimum of temperature in Dec. 1949 verified.
			273-month period graph, 1924 and 1947.
			Solar constant 1908-1920 backcasted. Reveals no correlation with Mount Wilson values but fairly good correlation with solar contrast values.
4088	1952	{ Smithsonian Misc. Coll., vol. 117, No. 10, fig. 6... p. 27... p. 29... p. 29... 1	Langley method for solar constant always gives individual day values too high or too low; only means of many days are reliable.

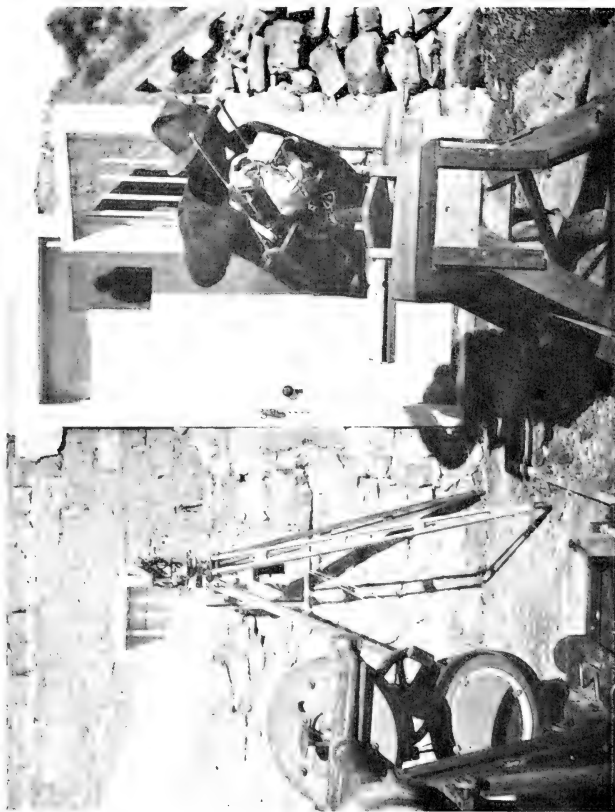
<i>Publ. No.</i>	<i>Reference</i>	<i>Subject</i>
4090	Smithsonian Misc. Coll., vol. 117, No. 11.....	Interferences with normals in weather records.
4103	Smithsonian Misc. Coll., vol. 121, No. 5.....	Solar variation and precipitation at Albany.
4135	Smithsonian Misc. Coll., vol. 122, No. 4.....	Meeting of professional meteorologists.
4211	Smithsonian Misc. Coll., vol. 128, No. 3.....	60-year weather forecasts.
4213	Smithsonian Misc. Coll., vol. 128 No. 4, pp. 12-13	Periodicities in solar variations.
4222	Smithsonian Misc. Coll., vol. 131, No. 1.....	Leading operations of the Astrophysical Observatory, 1895-1955.
4265	Smithsonian Misc. Coll., vol. 134, No. 1, pp. 15-17	Periods related to 273 months. Human pulse period of 212 days = 7.0 months \pm 0.5 percent, with subperiods $\frac{1}{2}$, $\frac{1}{3}$, $\frac{1}{6}$, $\frac{1}{7}$, $\frac{1}{11}$, all harmonics of 273 months. 7 months = $\frac{273}{39}$ months.
4338	Smithsonian Misc. Coll., vol. 135, No. 10.....	Periodicities in ionospheric data.
4352	Smithsonian Misc. Coll., vol. 138, No. 3.....	Long-range weather forecasting; exact length of master period 273 months.
4390	Smithsonian Misc. Coll., vol. 139, No. 9.....	Long-range forecast of U.S. precipitation.
4462	Smithsonian Misc. Coll., vol. 143, No. 2.....	16-day weather forecasts from satellite observations.
4471	Smithsonian Misc. Coll., vol. 143, No. 5.....	Long-range temperature forecast. See comparisons of accuracy of forecasts of precipitation in P. 4390 for large and small departures from the normal, p. 6.

SUPPLEMENTARY REFERENCES

- | | | | |
|------|---|---|---|
| 1957 | Smithsonian Contr. Astrophysics, vol. 3, No. 3... | 5 | Papers on the solar constant by Sterne, Abbot, Aldrich, and Hoover. |
| 1957 | Journ. Solar Energy Sci. and Eng., vol. 1, No. 1. | 7 | Weather and solar variation, Abbot. |
| 1958 | Journ. Solar Energy Sci. and Eng., vol. 2, No. 2. | 7 | Detailed procedure used in Abbot's method of long-range weather forecasting, Abbot. |



Smithsonian Observatory, Mount Wilson, Calif., with solar-constant outfit and tower telescope.



Smithsonian Observatory, Table Mountain, Calif. Observer with pyrheliometers and pyranometer.
Coelostat and theodolite for solar-constant work within.



Aldrich observing with double water-flow electric compensation pyrheliometer.



Boffin observing with silver-disk pyrheliometer.

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 146, NO. 4

EVOLUTIONARY TRENDS IN THE AVIAN GENUS CLAMATOR

By
HERBERT FRIEDMANN
Director
Los Angeles County Museum



(PUBLICATION 4532)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 30, 1964

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 146, NO. 4

EVOLUTIONARY TRENDS IN THE AVIAN GENUS CLAMATOR

By

HERBERT FRIEDMANN

Director

Los Angeles County Museum



(PUBLICATION 4532)

CITY OF WASHINGTON

PUBLISHED BY THE SMITHSONIAN INSTITUTION

OCTOBER 30, 1964

PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

CONTENTS

	Page
Acknowledgments	1
Introduction	2
Phylogenetic Relationships	6
Features of Brood Parasitism in <i>Clamator</i>	11
Host Selection and Its Evolution.....	14
Intensity of Parasitism.....	37
Egg Morphism	50
Incubation Period	57
Host-Parasite Nestling Relationship.....	58
Fledgling Feeding by Adult <i>Clamators</i>	61
Plumage Variations and Their Significance.....	62
Polymorphism	70
Migratory Behavior	75
Summary and Conclusions.....	92
Appendix—Additional Host Data.....	96
A. Data on the Hosts of <i>Clamator glandarius</i>	96
B. Data on Additional Hosts of <i>Clamator jacobinus</i>	103
C. Data on Additional Hosts of <i>Clamator levaillantii</i>	105
Bibliography	106

EVOLUTIONARY TRENDS IN THE AVIAN GENUS CLAMATOR

By HERBERT FRIEDMANN

Director, Los Angeles County Museum

ACKNOWLEDGMENTS

TO APPRAISE as accurately as possible the involved situations that exist in the species of *Clamator*, it was necessary to examine carefully large segments of the preserved material. Museum study skins were inspected to evaluate the nature, frequency, and distribution of the plumage phases, and the kinds and degrees of variation within these phases for possible suggestive clues as to their nature. The changes of plumages in all the included species were reviewed for possible phylogenetic hints they might reveal. And the eggs of the cuckoos and of their hosts were examined to determine the extent of adaptive similarity, or the lack of it, thus avoiding undue influence by earlier published opinions, some of which, as suspected, turned out to be casual and rather uncritical estimates, or were based on geographic segments of the total picture.

A research grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History enabled me to spend 3 productive weeks at the British Museum (Natural History) in London, where by far the largest assemblage of the pertinent material is stored, and also to spend a few days at the United States National Museum in Washington. To the custodians of these bird collections I express my thanks for their help.

By loan of actual specimens and by correspondence from cooperative curators of their respective collections, I have been able to tabulate the data on material of special interest in the museums of Bloemfontein, Bulawayo, Cape Town, Dundo, Durban, East London, Khartoum, King William's Town, Lourenço Marques, Nairobi, Pietermaritzburg, Port Elizabeth, Pretoria, and Salisbury, in Africa; of Bombay in Asia; of Basle, Berlin, Copenhagen, Genoa, Madrid, Milan, Paris, Stockholm, Turin, and Vienna, in Europe; and

of Ann Arbor, Baton Rouge, Berkeley, Cambridge, Chicago, Los Angeles, New Haven, New York, Philadelphia, Pittsburgh, and Princeton, in the United States. To the officials of all these museums, who have kindly sent me data or specimens, I hereby tender my thanks. The following individuals also have helped with observational notes and egg-specimen data: Salim A. Ali, M. Courtenay-Latimer, G. Duve, R. Kreuger, D. W. Lamm, R. Liversidge, G. R. Mountfort, J. Ottow, C. R. S. Pitman, C. G. Sibley, C. J. Skead, G. Symons, V. G. L. van Someren, J. G. Williams, and J. M. Winterbottom.

My personal field experience with *Clamator*, limited to the three species that occur in Africa, continued to play a contributing role in the present as in earlier studies. Acknowledgments, therefore, for the support that made these field studies possible are due again to the National Research Council, American Philosophical Society, the Guggenheim Foundation, and the Smithsonian Institution.

INTRODUCTION

The genus *Clamator* is one of a number of genera of cuckoos which are parasitic in their mode of reproduction. The vicissitudes of its biological history which are reviewed in this paper are of interest in clarifying some concepts involved in the overall problems of evolution of habits in the puzzling family Cuculidae.

Brood parasitism in the cuckoos is not a "single-line" development, as it is in the cowbirds, the honeyguides, or the ducks, but comprises many genera, some of which have evolved specialized features, such as the evicting habit in the nestling stage. Other genera have developed elaborate egg morphism with related host-specific gentes, some have an extremely restricted range of host species, others have a broader choice of fosterers, while still others show none of these refinements in their mode of reproduction. In the weaverbirds it is known that the parasitic habit has arisen independently in two sections of the family (Friedmann, 1960). Whether it arose equally independently in different groups of genera of parasitic cuckoos is still uncertain, but it has developed in various ways in the 18 genera that are parasites in their mode of reproduction.

These genera, each with its own special features and its own peculiar problems, are of much interest to the student of adaptation and evolution. C. D. Darlington (1953, pp. 441-443) wrote of the European cuckoo, *Cuculus canorus*, that it was ". . . uniquely instructive in its relations with the environment. Exposed from hatching to an alien environment for innumerable generations, the be-

haviour of the cuckoo, the instincts of the cuckoo, are determined by its heredity. Its migration and all its malpractices follow the pattern of a parent it has never seen.

"Further, of all animals, the female cuckoo most resembles man in exercising a choice which fixes her offsprings' environment . . . the cuckoo species is divided into mating groups which specialize in laying eggs in the nests of birds whose eggs theirs most closely resemble. The cuckoo species, like any large human community, thus has a spurious plasticity which derives from its variability. This variability, again like that of a human community, is preserved by natural selection, that is, by the adaptive value of a whole range of genetic types. The cuckoo is thus the most significant of all birds for the theory of heredity and environment . . ."

Without detracting from Darlington's estimate of the inherent philosophical importance of the biology of *Cuculus canorus*, it may be suggested that the present account of a group of that bird's less completely specialized relatives may even enhance it by presenting informative perspectives and tangential views into our total concept of brood parasitism in this family. There is a real need for this, since, in spite of the known differences in the mode of parasitism in the various genera of parasitic cuckoos, the literature of the subject is devoted largely to that one species, which, it so happens, is the most highly evolved and specialized of all the members of its family and possesses many features not present in other parasitic cuckoos. This has resulted in an overly accented, rather one-sided emphasis in the usual presentations and discussions of the subject. It is hoped that the present study may help to correct this and to offset some of the literature on cuckoo parasitism.

At the same time, the situation present in the four species of *Clamator* is, in itself, well worthy of study as a survey of the evolutionary history of a compact and relatively isolated genus of the family, only distantly related to *Cuculus*. The genus *Clamator* generally is considered fairly primitive; however, its included species reveal much adaptive evolution and the effects of diverse and not altogether harmonious trends. Not only is it a primitive group of highly specialized species but also one that reveals to a greater degree than most that evolution may proceed at different rates in different characters and in different species even within a small genus, and that some of these trends may even be abandoned after a state of high perfection had been achieved. In these respects this study differs from most.

The majority of studies of evolution within limited groups of animals emphasize single characters or single aspects, such as external morphology, relatively minor changes in size, shape, or proportions, or adaptation of one part or one structure to changing habits. Also, the stress has been placed on characters that seem to have gone the whole way from a generalized to a highly specialized condition. This emphasis is understandable—it is most convincing to be able to reconstruct historically the path or paths followed by piecing together carefully and critically all the available data. This procedure, however, has tended to conceal, or at least to detract attention from, the fact that many organisms have evolved only “part way,” and still have managed to survive and to succeed. This is, of course, generally implied or assumed in the stage elements of all more complete developments, but it is well to underscore it where, as in *Clamator*, some of the species have stopped at “part-way” stages.

The four species of the genus *Clamator* form a compact group that has been considered by Jourdain and Baker and other writers on parasitic cuckoos as one in which adaptive evolution in egg similarity to those of its usual hosts has gone as far as in any group of brood parasites. Yet, two of the four species have geographic segments (populations or races) that either never arrived at, or else appear to have “ignored” or to have “repudiated,” the results of the adaptive evolution of their respective stocks, and this situation has been arrived at in very different ways in the two.

Thus, in the case of the jacobin cuckoo, *Clamator jacobinus*, we have a species which, throughout its extensive Asiatic and part of its African range, is parasitic chiefly on babbling thrushes, most of which lay bluish eggs. In Asia and in northeastern Africa the eggs of the jacobin are always similarly bluish or blue-green in color, but in most areas south of the Sahara the resident jacobins, using some of the same type of hosts, but more frequently, bulbuls and shrikes, lay only pure white eggs, which contrast strikingly in appearance with those of their victims.

Turning to the great-spotted cuckoo, *Clamator glandarius*, we find that this species lays but one type of egg throughout its range. In the Iberian peninsula and adjacent parts of northwest Africa, it is almost exclusively parasitic on magpies, with the eggs of which its own show extreme similarity. So great, indeed, is the resemblance, that it has been cited frequently as an example of “perfected” adaptive evolution, and some not uncritical collectors have had the experience of collecting sets of eggs containing both species without realizing

this until later. However, in Egypt and in most of Africa south of the Sahara where there are no magpies, this cuckoo parasitizes crows of several species, and also it lays frequently in the dark, hole nests of starlings. Its eggs show little resemblance to those of these hosts.

If it could be demonstrated that the egg type of *Clamator glandarius* had evolved as an adaptation toward the use of magpies as hosts (it is the only species of *Clamator* laying speckled eggs, which egg type in cuckoos generally is considered an "advancement" from the more primitive unmarked eggs), then it would follow that the geographic spread of this cuckoo to areas where there are no magpies would appear to be a matter involving something akin to a "repudiation" of the specialization it had achieved earlier through natural selection with the magpie as the effective agent. This, if established, would open a rare opportunity to study the biology of a highly adapted species in a new environment where this adaptive excellence no longer is a special advantage, but where it is apparently no critical encumbrance with new and nonadapted hosts.

In attempting to trace the course of the evolution of a group of organisms, or of a habit and its correlated morphological characters, it is a common experience to find that the trend generally is toward a more and more perfected stage of adaptation, eventually reaching a degree of perfection beyond which it cannot, or at least does not, go. From the general to the specialized, from the "good enough to survive" to the obviously advantageously adapted, seems to be the history of case after case. What is unusual is to find a highly adapted evolutionary product apparently *departing* from the particular set of conditions which its past history appears to have been concerned in meeting more effectively, and carrying with it in its secondary path the primary adaptations no longer needed or especially advantageous to it.

On the other hand, if it should seem more likely that the great-spotted cuckoo developed its speckled-egg type south of the Sahara, and subsequently spread to Mediterranean areas, where its egg happened to "fit" so well with those of a new host, this would have to be considered as a most unusual instance of preadaptation. It should be kept in mind, however, that the known facts concerning host egg similarity, or mimicry, in parasitic cuckoos generally cannot be explained satisfactorily on the basis of any assumed preadaptations, but, on the contrary, indicate the degree to which real adaptations in egg coloration have been evolved.

The situation in the jacobin cuckoo is just the opposite. The seemingly similar success of the white-egg laying population with that

of the blue-egg layers raises the problem of the efficiency as selective agents of the relatively uniformly blue-egg laying hosts.

Inasmuch as host adaptation is an important part of the biology of brood parasitism, the picture in *Clamator* commends itself for careful study and interpretation. This is attempted in the present report. Still other biological problems, similarly apparently arrested in their development as "part-way" stages in the species of *Clamator*, concern development of plumage morphisms and of migratory behavior. Thus, in two of the four species we find geographically delimited melanistic plumage phases, more restricted in range in one than in the other, but in neither has the black morph replaced, or achieved reproductive isolation from, the pale, or normal, morph. Also, all four species are migratory in parts of their total respective ranges and not in other parts. The extent of migratory movement within a single species varies from none at all to thousands of miles. Geographic segments of each, not necessarily even subspecifically distinct, differ markedly from other conspecific segments in this important trait. These are also discussed with all available evidence in the following pages.

The four species of crested cuckoos comprising the genus *Clamator* form a group of birds that still reveal much—that in other groups has been concealed—in their continued progress toward greater adaptive excellence.

PHYLOGENETIC RELATIONSHIPS

The genus *Clamator* contains four species of crested cuckoos of Africa, Asia, and parts of Mediterranean Europe (fig. 1)—*jacobinus*, *levaillantii*, *coromandus*, and *glandarius*. It forms a natural, easily recognized group, characterized by a well-developed occipital crest of elongated feathers, by a transilient mode of remigial molt, and by the nares in the form of linear ovals. It agrees with the subfamily Cuculinae in being parasitic in its breeding, but lacks the evicting behavior pattern in its young. It agrees with the Cuculinae in most other characters, but varies from that group in the direction of the Phaenicophaeinae in having only 13 cervical vertebrae (14 in the Cuculinae and in the other subfamilies of cuckoos), and in having the muscle formula "ABXYAm" (Berger, 1960). No one has proposed merging it with any other genera, and practically all of its recent investigators (Stuart Baker, Berger, Friedmann, Jourdain, Peters, the Stresemanns, etc.) have generally agreed that it is a primitive group in its particular subfamily, the Cuculinae. This is

FIG. 1.—Geographic range of *Clamator*.

the subfamily that not only contains most of the genera of parasitic cuckoos (all but the two Neotropical *Tapera* and *Dromococcyx*), but also contains no cuckoos that are not parasitic, as do the other five subfamilies. In their recent study of the molting patterns of the cuckoos, the Stresemanns (1961) have pointed out also the primitive nature of *Clamator's* transilient mode of remigial molt, and have mentioned the absence of evicting behavior in its young as another evidence of primitiveness. Peters (1940) seems to have been so convinced of the primitive nature of the genus *Clamator* that he actually placed it at the very beginning of his list of all the members of the family.

While I also conclude that the crested cuckoos are to be looked upon as among the primitive, oldest sections of the subfamily Cuculinae, I doubt that this subfamily may justifiably be placed at the base of the whole family. Inasmuch as nest-building, incubation of eggs, and care of young are features of reproductive activity in practically all groups of birds, it seems likely that the most primitive cuckoos were nonparasitic as well. From this it follows that a subfamily made up wholly of brood parasites could not be the most primitive section of a family that contains many self-breeding genera and species.

The age of the genus *Clamator* is, of course, unknown, but some suggestive evidence points to its being not later than Pliocene in origin. This is an inference based on the fact that although the genus occurs over a wide area in Africa and in southern Asia, it is absent in the Malagasy Republic (formerly Madagascar). In his study of the history of the African terrestrial fauna, Lönnberg (1929) concluded that Pliocene faunal transfers between southern Asia and Africa generally are absent from the Malagasy Republic regardless of the extent of their range in either of the two continents. The fact that *Clamator* does not occur in Malagasy suggests that the spread of the genus probably took place during, or subsequent to, the Pliocene, at which time Malagasy became completely isolated as an oceanic island. As a result of the present study, it appears that the southern African population of *C. jacobinus* is the oldest, most primitive of existing *Clamator* stocks, and it seems that its species spread throughout much of Africa and thence to Asia. The fact that in southern Asia this stock gave rise to a more involved evolutionary development than in Africa, and eventually produced so different a bird as *C. coromandus*, which, in turn, seems a stage on the phylogenetic road that culminated in *C. glandarius*, suggests a very considerable antiquity for the genus in

Asia. The need for sufficient time makes a Pliocene spread more probable than a post-Pliocene infiltration, presuming, of course, a Pliocene or pre-Pliocene origin of the group stock in southeastern Africa.

The fossil record of the Cuculidae gives no pertinent data. The family is known from the Oligocene of France (*Dynamopterus velox*), from the middle Miocene (*Necornis*, only questionably a cuckoo), and from numerous Pleistocene remains too recent to be of any use in reconstructing the history of the family (*Coua*, *Cuculus*, *Geococcyx*, *Coccyzus*, *Crotophaga*, *Tapera*, and *Pyrhrococcyx*), but even there nothing close to *Clamator*.

It is not feasible to say, or even to guess, from what stock *Clamator* may have evolved, as there are no living cuckoos that seem likely ancestral forms. Yet I cannot put down the vague thought that something like the Phaenicophaeinae in Asia, or like *Ceuthmochares* in Africa today, may be closer to—less subsequently specialized and hence less deviated from the original—primordial stock of the family, and to this extent may be looked upon as existing representations of the ancestral group that gave rise to *Clamator*.

Recent studies by Berger (1960, p. 82), especially his myological dissections, coupled with his familiarity with what had been written of the breeding habits, parasitic or otherwise, of the genera of cuckoos, led him to write as follows “. . . It would appear that one must discount either myological data or breeding behavior in deciding the relationships among the cuckoos . . . Thus, if we are to place any value on morphological characters, we must assume either that parasitism has developed independently as many as four times in this one family (which seems highly unlikely) or that the parasitic habit (or tendency for it) developed in the primitive cuckoos (all ABXYAm) . . .” Similarly, Darlington (1957, p. 273) concluded from a study of the geographic distribution of the cuckoos as a whole, that the family is probably ancient and had a “. . . complex, undecipherable history.”

Although there is fairly good agreement among students that *Clamator* is a primitive genus, there is no such concurrence as to what other living genera it is closest in its phylogenetic relations. The Stresemanns (1961, p. 328) concluded that *Clamator* was only distantly related to the other Cuculinae. Many years ago, Sharpe (1872, p. 68) suggested it was somewhat similar to *Eudynamis*, but this is not substantiated by Berger's anatomical findings (1960). He noted that there were two basic types of cuculine muscle formulae,

and that *Clamator* was of one type, along with such genera as *Cuculus*, *Chrysococcyx*, *Surniculus*, *Tapera*, and others, while *Eudynamis* was of the other, along with *Scythrops* and *Dromococcyx*. It must be admitted that it is not wholly clear how significant this myological character may be, as each group contains genera that seem only distantly interrelated. Thus, in the former aggregate, *Tapera* is very different from the rest, and in the latter group all three genera are widely separated.

Berger's anatomical studies, together with earlier work by Beddard, Forbes, Fürbringer, and others, give us our best evidence of relationships within the family. All the characters, osteological, myological, and even ecdysial, have one thing in common—they are all of sufficiently nonfunctional nature as to make them seem relatively removed from the effects of selection. Hence they may be looked upon as phylogenetically conservative, and, to that degree, they are reliable indices of relationship. Breeding habits, parasitic or otherwise, are more amenable to change. In fact, one of the safest deductions that may be made from a study of brood parasitism is that in all the groups in which it occurs it is a secondary situation that arose in stocks that were originally self-breeding.

Inasmuch as all the members of the Cuculinae are parasitic, it would seem that brood parasitism had already become established in their common, remote, ancestral stock before they became differentiated into the genera as we know them today. This differentiation has resulted in a wide variety of end products, some 16 genera with 46 species according to Peters' list (1940), which suggests a long period for its operation. This, in turn, indicates a great antiquity of brood parasitism in the group, an antiquity that the history of *Clamator* suggests must date from pre-Pliocene or not later than Pliocene time.

In studying the genus *Clamator* we are fortunate in that considerable information is available on the life histories of each of its four species. The entire group has been considered by Baker and by Jourdain, two of the principal students of cuckoos' eggs, as one in which adaptive evolution in egg similarity to those of its usual hosts has progressed as far and as successfully as in any genus of cuckoos. *Clamator* is, therefore, a primitive group of highly evolved species, a biological situation that is not infrequent despite its seemingly paradoxical nature. As Baker (1942, p. 3) put it, "... perfection or completeness in adaptation or evolution must depend upon time ... and therefore the most perfectly evolved egg need not and does

not belong to the most perfectly advanced Cuckoo. The more primitive forms of parasitic Cuckoo, such as members of the genus *Clamator*, containing the Great Spotted Cuckoo, have probably had an infinitely longer existence in their present form and condition than such beautifully perfected forms as our Common Cuckoo, and we should therefore expect primitive Cuckoos to have acquired a more perfect adaptation in their eggs than those Cuckoos more highly developed."

The phylogenetic relationships of the species of *Clamator*, as suggested by all the data brought together in this paper, ethological, morphological (chiefly plumage coloration and eggshell pattern), and distributional, as shown in the diagram (fig. 2), reveal that *jacobinus*

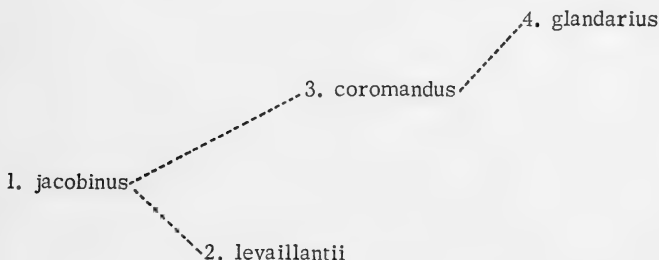


FIG. 2.—Relationships within the genus *Clamator*.

is the most primitive member, and that from it two lines of descent bifurcated. One, rather short one, led to *levaillantii*; the other longer one led to *coromandus* and from this to the "climax" species, *glandarius*. The geographic movements undergone by *Clamator* during its differentiation and dispersal are shown in figure 3.

FEATURES OF BROOD PARASITISM IN CLAMATOR

The genus *Clamator* evolved from an earlier stock that was already parasitic, as is indicated by the fact that all of its species are parasitic. It is understandable, therefore, that a comparative survey of their habits affords no clues as to the origin of this mode of reproduction, although it does reveal much of the course of the development parasitism underwent in this particular genus.

Compared with a highly specialized group, such as the species of *Cuculus*, *Clamator* is relatively simpler and shows none of the development of infraspecific gentes, each with its elaborate, adaptive egg



FIG. 3.—Evolutionary dispersal of *Clamator*.

1. Dispersal of *C. jacobinus* from southeast Africa to most of Africa and to India. 2. Dispersal of *C. levaillantii*. 3. Dispersal of *C. crenatus*. 4. Ancient dispersal of *C. levaillantii* from southeast Africa to Europe and North America. 5. Recent dispersal of *C. levaillantii* from southeast Africa to the Caribbean and North America.

morphism, and none of the instinctive eviction of nestmates by the newly hatched young, so characteristic of some species of *Cuculus*. Also, compared with the latter genus, all four of the species of *Clamator* are far more prone to deposit multiple eggs in individual host nests, either multiple eggs by the same cuckoo or multiple use of the same nest by several cuckoos. These differences suggest that the refinements shown in *Cuculus* are evolutionary advances over the basic cuculine stock and that *Clamator* is nearer to the original, common ancestor in these matters. This lack of conformity or control in egg deposition led Mountfort (1958, pp. 54-56) to conclude that ". . . the parasitic behaviour of the Great Spotted Cuckoo is in many respects more complicated than that of our familiar Cuckoo, in which the single nestling merely evicts its foster-brothers from the nest . . ." It seems truer to say that the "uncomplicated" behavior of *Cuculus canorus* is a result of much adaptive evolution, whereas the "complicated" picture in *Clamator glandarius* still retains much of the simpler, less-developed features of the basic primitive parasitic cuckoo that we may postulate as the remote source of both genera. In my introductory statement I mention that the entire literature and thinking about cuckoos is overly dominated by *Cuculus canorus*. If specific evidence were needed to demonstrate this, Mountfort's statement about *Clamator glandarius* would be a case in point.

All the species of *Clamator* have the habit, common to so many parasitic cuckoos, of removing one or more of the host eggs from the nests of their victims either before or after laying in them. Occasionally this does not take place, and in some nests some of the host eggs are dented (equivalent, in survival terms, to destroyed) by the beak or the claws of the adult parasite. There are ample observational data on this in three of the species—*jacobinus*, *coromandus*, and *glandarius*. The lack of such records for *levaillantii* is not significant. There is no need to repeat here these observations as they are already on record in my earlier (1949a, 1956) accounts, and in that of Stuart Baker (1942). Particular mention may be made, however, of Mountfort's observations (Mountfort, 1958, pp. 54-56; Mountfort and Ferguson-Lees, 1961, pp. 98-99), one of the few detailed recent contributions on this habit in *C. glandarius*. They marked eggs with indelible ink so as to be able to identify them individually on consecutive days; they found that when the hen cuckoos laid they removed one and sometimes two of the magpie's eggs. In no instance did they remove eggs laid by other great-spotted cuckoos, which raises the question as to whether they could recognize

the small differences in the eggs. Mountfort and Ferguson-Lees found that as many as three cuckoos laid in one nest.

The various topics of interest in the brood parasitism of *Clamator* are discussed in detail below (pages 14 to 62).

HOST SELECTION AND ITS EVOLUTION

A study of the four species of *Clamator* yields considerable data relevant to the evolutionary changes that formed their present host preferences. Not only are the hosts of each fairly definitely restricted in kind, but two of the four parasites show unmistakable signs of changes in their selection of favored fosterers. To this extent they afford glimpses of the past development of their host orientation, a basic part of their parasitic mode of reproduction. The two that show these signs of evolutionary change are *C. jacobinus* and *C. glandarius*, the most primitive and the most advanced members of the genus. In both species, the change took place together with extensive geographic expansion of their ranges. Furthermore, on the basis of the total survey it is possible to sense the course of host selection in the other two *Clamators* as well.

Clamator jacobinus (figs. 4, 5, pp. 15, 16)

The presumed ancestral home of the pied cuckoo, *C. jacobinus*, is in southeastern Africa, the area now inhabited by the race *serratus*. In this region, ranging from Cape Province, Natal, Transvaal, Orange Free State, parts of South-West Africa, and Bechuanaland, to Southern and Northern Rhodesia and Nyasaland, the cuckoo has been found to lay its eggs in the nests of 22 species, but 13 of these have been recorded as hosts but once, and 2 others but twice. The only species definitely known to be frequent and regular fosterers are four species of bulbuls of the genus *Pycnonotus* (*nigricans*, *barbatus*, *capensis*, and *importunus*) and two shrikes, *Lanius collaris* and *Telophorus zeylonus*. These 6 hosts account for 101 of the total 123 cases of parasitism by *serratus* known to me.

When the pied cuckoo began its geographic expansion, giving rise to the race *pica* in equatorial and northeastern Africa and in India, the population inhabiting these new areas turned from bulbuls and shrikes to babblers as their chief fosterers. The race *pica* has been found to parasitize some 36 species of birds, half of which have been so recorded but a single time. No fewer than 26 of the known hosts are babblers, and all the hosts for which there are 5 or more records are species of this group. More than four-fifths of all instances of

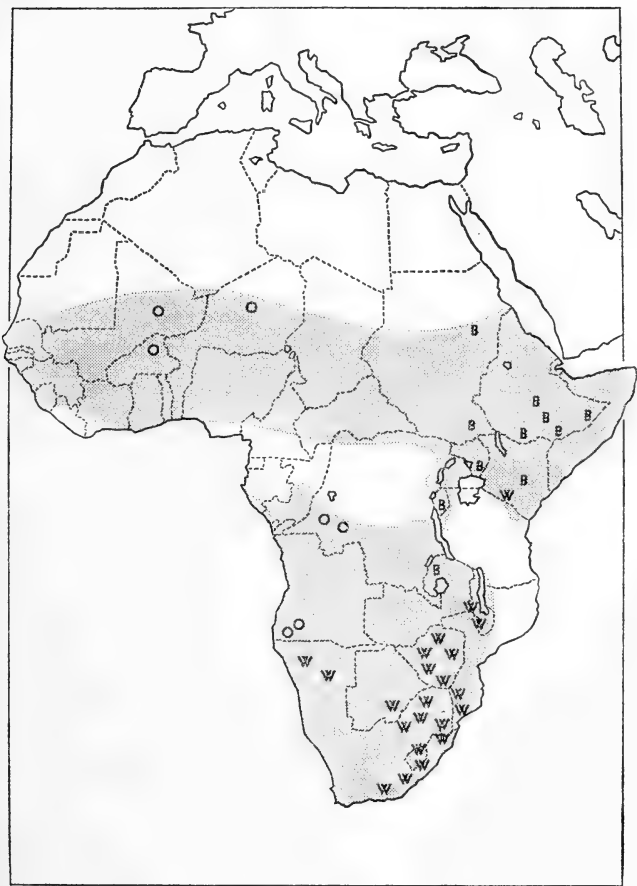
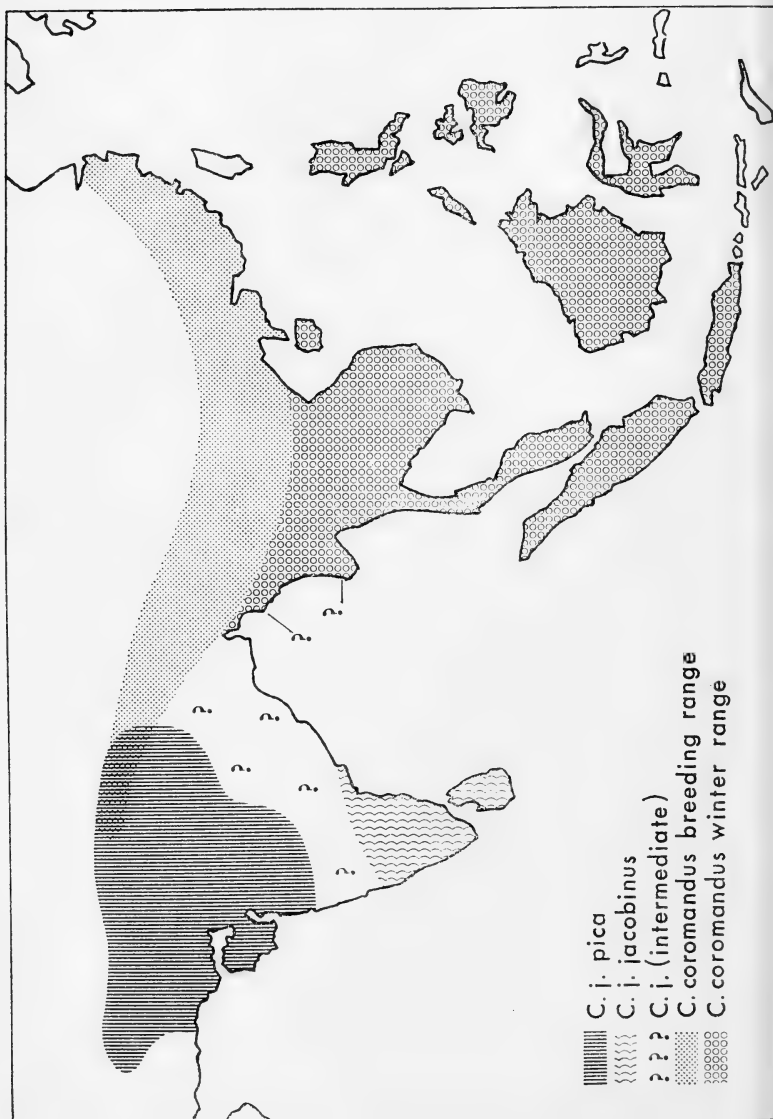


FIG. 4.—African range of *Clamator jacobinus*.

W, White egg record. B, Blue egg record. O, Egg of unrecorded color.



parasitism by *pica* known to me refer to 7 species of babblers (94 out of a total of 106 nests) of the genera *Garrulax* (*moniligerus*, *pectoralis*, *delesserti*, and *erythrocephalus*) and *Turdoides* (*caudatus*, *striatus*, and *affinis*).

It may be stressed that inasmuch as several species of bulbuls, shrikes, and babblers occur as breeding birds in considerable numbers throughout the ranges of both races of the pied cuckoo, the difference in host selection is not something imposed on the parasites. In Kenya the race *pica* has been noted by van Someren (*in litt.*) to lay fairly frequently in the nests of a bulbul, *Pycnonotus barbatus*, (3 records), but in India there is but a single instance of a bulbul nest used by the parasite. Inasmuch as Kenya was an early area of invasion in the course of the northward spread of *C. jacobinus*, this tendency there to use bulbuls as fosterers may have been established very early prior to the general shift to babblers. As discussed more fully elsewhere (pp. 51-53) the egg of *pica* is greenish blue whereas that of *serratus* is pure white.

In India, where the pied cuckoo has been studied extensively, Baker (1942, p. 82) had no records of its eggs in central or southern India from any nests other than those of babblers, though a few such had been reported by others. It so happens that this cuckoo, after becoming well established in India, began to expand its range northward into the foothills of the Himalayas. Baker noted that "when we come to the hills . . . we find the . . . Pied Crested Cuckoo placing their eggs in a great range of birds' nests, though in most cases these are nests of the Larger Laughing-Thrushes, nearly all laying blue eggs with which the eggs of the Cuckoos do not contrast. The normal fosterers here are undoubtedly the Necklaced and Black-gorgeted Laughing-Thrushes in the Eastern Himalayas and the Striated Laughing-Thrush in the Western. Of eggs laid in these nests I have 49, while I have 42 deposited in the nests of twelve other Laughing-Thrushes . . . With the exception of the species mentioned . . . I do not believe any of the others could be considered normal fosterers, while even these three can only be considered normal because they have been selected as such by birds breeding outside their own normal Plains area. . . ."

In Africa, when *C. jacobinus* stock gave rise to what has evolved into *C. levaillantii*, that new group, even more than the more northern *jacobinus* (now *pica*), became attached to babblers in its brood parasitism. In these birds, *C. levaillantii* found an abundant supply of fosterers and in their use found an escape from competition with its

long-established ancestral relative. To this day *C. levaillantii*, as we shall see, is parasitic chiefly on babblers. In India, when the *C. jacobinus* stock gave rise, apparently in the northern part of its range in the foothills of the Himalayas, to what has become *C. coromandus*, the trend shown in the relatively recent use of laughing-thrushes by northern *jacobinus* became well established in the new group. We find today that laughing-thrushes, chiefly of the genus *Garrulax* are the mainstay of *C. coromandus*.

The tabular list of the known fosterers for each of the three races of the pied cuckoo shows the remarkable degree to which the hosts of the African *serratus* and the Indian *pica* and *jacobinus* differ. The picture is not as clear in the case of the African population of *pica*, as data on it are still rather sparse, and involve only five species of hosts—a bulbul, *Pycnonotus barbatus*, three babblers of the genus *Turdoides* (*fulvus*, *rubiginosus*, and *leucopygia*), and a shrike, *Telophorus zeylonus*. It may be expected that more extensive observations will add further Timaliine fosterers to this list, as there is no reason to suppose that African *pica* differ from Asiatic ones in their type of host choice.

HOSTS OF CLAMATOR JACOBINUS

Host	<i>serratus</i>	<i>jacobinus</i>	<i>pica</i>
<i>Stigmatopelia senegalensis aequatorialis</i>	x
<i>Centropus grillii wahlbergi</i>	x
<i>Halcyon albiventris albiventris</i>	x
<i>Colius striatus minor</i>	x
<i>Colius indicus indicus</i>	x
<i>Dicrurus adsimilis adsimilis</i>	x
<i>Campephaga phoenicea flava</i>	x
<i>Pycnonotus cafer bengalensis</i>	x
<i>Pycnonotus nigricans</i>	x
<i>Pycnonotus capensis</i>	x
<i>Pycnonotus barbatus layardi</i>	x
<i>Pycnonotus barbatus fayi</i>	x
<i>Pycnonotus barbatus tenebrior</i>	x
<i>Pycnonotus importunus importunus</i>	x
<i>Pycnonotus importunus noomei</i>	x
<i>Phyllastrephus terrestris terrestris</i>	x
<i>Aegithina tiphia humei</i>	x
<i>Turdoides caudatus caudatus</i>	x
<i>Turdoides earlei earlei</i>	x
<i>Turdoides longirostris</i>	x	...
<i>Turdoides malcolmi</i>	x
<i>Turdoides subrufus subrufus</i>	x
<i>Turdoides striatus sindianus</i>	x

HOSTS OF CLAMATOR JACOBINUS (continued)

<i>Host</i>	<i>serratus</i>	<i>jacobinus</i>	<i>pica</i>
<i>Turdoides striatus somervillei</i>	x
<i>Turdoides striatus malabaricus</i>	x
<i>Turdoides striatus striatus</i>	x	x
<i>Turdoides striatus rufescens</i>	x	...
<i>Turdoides fulvus acaciae</i>	x
<i>Turdoides rubiginosus rubiginosus</i>	x
<i>Turdoides jardinei natalensis</i>	x
<i>Turdoides affinis affinis</i>	x
<i>Turdoides leucopygia omoensis</i>	x
<i>Babax lanceolatus woodi</i>	x
<i>Garrulax moniligerus moniligerus</i>	x	x
<i>Garrulax pectoralis pectoralis</i>	x	x
<i>Garrulax pectoralis meridionalis</i>	x	...
<i>Garrulax striatus striatus</i>	x
<i>Garrulax striatus brahmaputra</i>	x
<i>Garrulax leucolophus leucolophus</i>	x
<i>Garrulax delesserti gularis</i>	x
<i>Garrulax ruficollis</i>	x
<i>Garrulax merulinus merulinus</i>	x	...
<i>Garrulax caerulatus subcaerulatus</i>	x
<i>Garrulax cachinnans cachinnans</i>	x	...
<i>Garrulax lineatus lineatus</i>	x
<i>Garrulax austeni austeni</i>	x
<i>Garrulax squamatus</i>	x
<i>Garrulax erythrocephalus chrysopterus</i>	x
<i>Garrulax phoeniceus bakeri</i>	x
<i>Actinodura egertoni khasiana</i>	x
<i>Alcippe nipalensis nipalensis</i>	x	x
<i>Parisoma subcaeruleum subcaeruleum</i>	x
<i>Copsychus saularis saularis</i>	x
<i>Cinclidium leucurum</i>	x
<i>Enicurus maculatus guttatus</i>	x	x
<i>Monticola rufiventris</i>	x
<i>Myophonus caeruleus temminckii</i>	x
<i>Zoothera citrina citrina</i>	x	x
<i>Sigelus silens</i>	x
<i>Terpsiphone viridis perspicillata</i>	x
<i>Sphenoeacus afer transvaalensis</i>	x
<i>Motacilla capensis capensis</i>	x
<i>Motacilla aguimp vidua</i>	x
<i>Laniarius ferrugineus natalensis</i>	x
<i>Telophorus zeylonus zeylonus</i>	x
<i>Telophorus zeylonus phanus</i>	x
<i>Lanius schach tricolor</i>	x
<i>Lanius schach nigriceps</i>	x	...
<i>Lanius collaris collaris</i>	x
<i>Petronia superciliaris superciliaris</i>	x

One important point, not revealed by the tabulation, is the relative frequency with which the different hosts are selected. Out of the total 123 African records, 59 are of species of the genus *Pycnonotus*, and 14 more are of other bulbuls, making a total of 73, or almost 60 percent of the total, that refer to this one family of hosts; 23 are of one species of *Lanius*, and 10 more are of other shrikes, a total for this family of 33, or more than 25 percent of the total; only 5, or not quite 5 percent, are of babblers. On the other hand, out of 106 Asiatic records, only 1 is of a *Pycnonotus*, but over 85 percent are of babblers, chiefly of the genera *Turdoides* and *Garrulax*.

The figures given above for the frequency of parasitism on bulbuls and shrikes in Africa are actually below the truth, as they are based solely on the total of individual instances reported. They make no allowance for the undocumented, general statements of experienced collectors, such as Plowes (1944, p. 93), who wrote that practically every bulbul nest examined was found to contain one or more eggs of the jacobin cuckoo. Also, generally a lower percentage of cases of parasitism on frequent hosts gets into the literature because of their repetitive nature, whereas practically all cases of infrequent ones are apt to find their way into print eventually.

As may be seen from the list of fosterers, in the great majority of cases the pied crested cuckoo lays its eggs in open, cup-shaped nests built in trees or bushes. The one record of its using a kingfisher as a host (Schönwetter, 1928, p. 130) and the two involving the rock sparrow, *Petronia* (de Klerk, 1942, p. 58), are the only instances of its parasitizing hole-nesting species. Another unusual type of nest choice is the lone case of a coucal, *Centropus grillii wahlbergi*, as a host. This bird builds a roofed-over, or domed, nest of fine twigs and grasses, on the ground. Other frequently terrestrial-located nests known to be used occasionally are those of two species of wagtails, *Motacilla capensis capensis* and *Motacilla aguimp vidua*, and of the grass-bird, *Sphenoeacus afer transvaalensis*.

In the present state of our knowledge of *Clamator jacobinus* the only obvious difference in its overall "fitness" to all the aspects of its existence in India and northeastern Africa on the one hand, and in southern Africa, on the other, is the much lesser degree of adaptive similarity of its eggs to those of its common hosts in the latter area. Strangely enough, in the areas where there is adaptive similarity it appears to have value to the parasite, but in the areas where it is

nonexistent its absence seems quite unimportant. Baker's data (1942, p. 83) on this cuckoo in India reveal a strong correlation between percentage of host acceptance of its eggs and the degree of egg resemblance involved, and, conversely, between the incidence of rejection when the cuckoos' eggs are deposited in nests of nonadaptive hosts and the degree of difference in the eggs of the two. Thus, of 106 parasitized nests of "normal" (*i.e.*, egg-adapted) fosterers, only 1 was deserted (less than 1 percent); of 48 parasitized nests of "unusual" fosterers, 3, or 6.25 percent were deserted; of 8 parasitized nests of "abnormal" fosterers, 5, or 62.5 percent, were deserted. Similar figures were found (Baker, 1942, p. 85) for the red-winged crested cuckoo, *Clamator coromandus*: of 111 "normal" fosterers' nests, 1, or 0.9 percent was deserted; of 58 "unusual" fosterers' nests, 4, or 6.9 percent were deserted; of 12 "abnormal" fosterers' nests, 6, or 50 percent were deserted.

In the case of the jacobin cuckoo in southern Africa no such correlation has been found. In fact, the most frequently imposed upon hosts in South Africa are two bulbuls, *Pycnonotus nigricans* and *P. barbatus*, whose eggs are salmon to pinkish white, blotched and blurred with reddish brown and grayish lavender, very different from the pure white eggs of the local race of the jacobin cuckoo. Yet these bulbuls accept and incubate these dissimilar eggs. Perhaps the next commonest host in that area is the fiscal shrike, *Lanius collaris*, whose eggs also differ from those of the parasite about as much as do those of the bulbuls, being grayish green rather than pink, but equally speckled and blotched with brown and lilac. The fact that this shrike accepts the strange eggs is even more surprising, as it is an aggressive bird that has been known to attack and to drive off the cuckoos when they come too close to its nest. Yet, in spite of this, once the eggs are deposited in the nest, the seemingly alert, pugnacious host appears to be indifferent to their appearance.

***Clamator levillantii* (fig. 6, p. 22)**

The stripe-breasted cuckoo is the least known member of the genus, but while the total number of observed instances of its parasitism is less than that of the others, it is sufficient to show a marked preference for babblers as fosterers. The list includes 10 species, 6 of which are babblers, and which, together, account for more than three-fourths of all the records. In fact, one species, *Turdoides jardinei*, alone, with

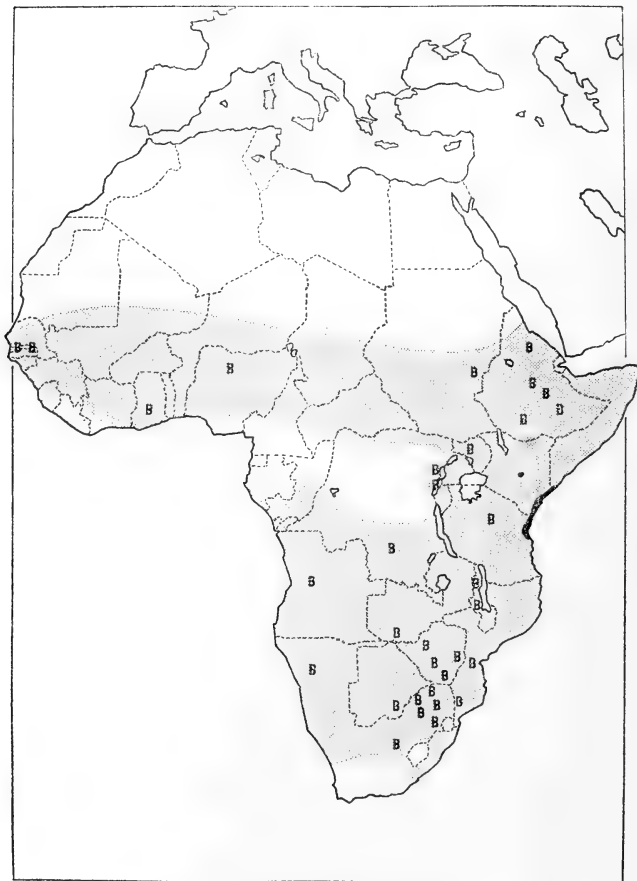


FIG. 6.—Range of *Clamator levaillantii*.

B, Breeding record. Solid black area denotes region of polymorphism.

some 23 records, account for half of the total. The known hosts are as follows:

<i>Phoeniculus purpureus zuluensis</i>	<i>Turdoides jardinei jardinei</i>
<i>Colius striatus striatus</i>	<i>Turdoides jardinei natalensis</i>
<i>Pycnonotus barbatus minor</i>	<i>Turdoides jardinei kirki</i>
<i>Pycnonotus barbatus layardi</i>	<i>Turdoides jardinei emini</i>
<i>Phyllanthus atripennis bohndorffi</i>	<i>Turdoides jardinei tanganjicae</i>
<i>Turdoides plebeja gularis</i>	<i>Turdoides reinwardii reinwardii</i>
<i>Turdoides plebeja cinereus</i>	<i>Turdoides leucopygia hartlaubii</i>
<i>Turdoides plebeja plebeja</i>	<i>Turdoides bicolor</i>
<i>Turdoides plebeja platycircus</i>	<i>Cossypha caffra caffra</i>

Of these 10 species, the first is not more than an accidental choice, and is based on a questionable identification of the parasitic egg (Roberts, 1939a, pp. 10-13). In addition to these it may be added that Bradfield (1931, pp. 7-9) suggested that in Damaraland the Burchell starling, *Lamprolornis australis*, was also parasitized, but he had no evidence other than that he had noted these starlings "mobbing" a stripe-breasted cuckoo.

Clamator coromandus (fig. 5, p. 16)

The red-winged cuckoo is parasitic chiefly on babblers, and, within this group, primarily on the larger laughing-thrushes of the genus *Garrulax*, some 13 species of which have been found to be victimized. Baker (1942, pp. 196-197) listed 265 eggs of the red-winged cuckoo in his collection, taken from nests of 21 species (25 species and subspecies) of hosts. Of these 265, all but 24 were found in nests of *Garrulax*, and no fewer than 109 from nests of a single species, the necklaced laughing-thrush, *G. moniliger*, and 37 from nests of the black-gorgeted laughing-thrush, *G. pectoralis*.

Our knowledge of this cuckoo's fosterers is still largely based on collections and observations from the Indian and Burmese portions of its range. In due time many hosts from other areas will be added to the list. The following list of known victims is based on that of Baker, with a few additions from other sources.

<i>Dicrurus adsimilis macrocerus</i>	<i>Garrulax delesserti gularis</i>
<i>Pomatorhinus erythrogenys maclellandi</i>	<i>Garrulax cineraceus cineraceus</i>
<i>Turdoides gularis</i>	<i>Garrulax rufogularis assamensis</i>
<i>Garrulax moniligerus moniligerus</i>	<i>Garrulax caerulatus subcaerulatus</i>
<i>Garrulax moniligerus fuscatus</i>	<i>Garrulax ruficollis</i>
<i>Garrulax pectoralis pectoralis</i>	<i>Garrulax merulinus merulinus</i>
<i>Garrulax pectoralis meridionalis</i>	<i>Garrulax squamatus</i>
<i>Garrulax striatus striatus</i>	<i>Garrulax erythrocephalus chrysopterus</i>
<i>Garrulax striatus brahmaputra</i>	<i>Garrulax phoeniceus bakeri</i>
<i>Garrulax leucolophus leucolophus</i>	<i>Actinodura egertoni khasiana</i>
<i>Garrulax leucolophus belangeri</i>	

Copsychus saularis saularis
Enicurus schistaceus
Myiophonus caeruleus temminckii

Zoothera citrina citrina
Turdus protomelas
Lanius schach tricolor

As we have already noted, when the Indian population of pied cuckoos (*pica*) began extending their range northward into the foothills of the Himalayas and found themselves removed from the habitat of the babblers of the genus *Turdoides* that had served them as fosterers in the plains, they began using the larger species of *Garrulax*. This change was probably already incipient in the *pica* stock, as it had become very pronounced and fixed in the earlier evolutionary offshoot from *pica* that resulted in *C. coromandus*. There must certainly have been a considerable time span involved in the evolution of the red-winged from the pied cuckoo, whereas the northward spread of the latter seems to have been fairly recent.

***Clamator glandarius* (fig. 7, p. 25)**

The great-spotted cuckoo is the most advanced of the four species of *Clamator*, and is closer to *C. coromandus* than to either of the others. From the circumstantial evidence of the current situation in the genus, it is justified to conclude that *glandarius* was an evolutionary development from the stock at present represented by *coromandus*. Hence, it seems probable that it originated somewhere near the north-eastern portion of the range of that species. Moving eastward, the primordial *glandarius* came into contact with magpies, a group of sizable, suitable, potential fosterers until then unaffected by any parasitic cuckoo, and to them it became adapted with marked success. Advancing farther eastward *glandarius* met with magpies in southern Iran, Iraq, Lebanon, etc., in areas of warmer climate than the Himalayan foothills and slopes of northern Assam, Bhutan, and Sikkim, where its ancestors may have first encountered their magpie hosts. In fact, the presence of the latter birds may well have expedited the eastward shift of early *glandarius*. Being essentially a warm climate form, *glandarius* left its original locus and eventually became a circum-Mediterranean species, still largely in areas of sympatry with the magpie, although becoming allopatric with it in eastern Egypt, where it used crows as hosts instead. At that stage of its history *glandarius* was largely contained within the range of its magpie host, and its great spread to sub-Saharan Africa, completely away from this fosterer, came much later.

It is conceivable, though, in the nature of things not demonstrable, that possible competition from the corvine parasitism of the koel,

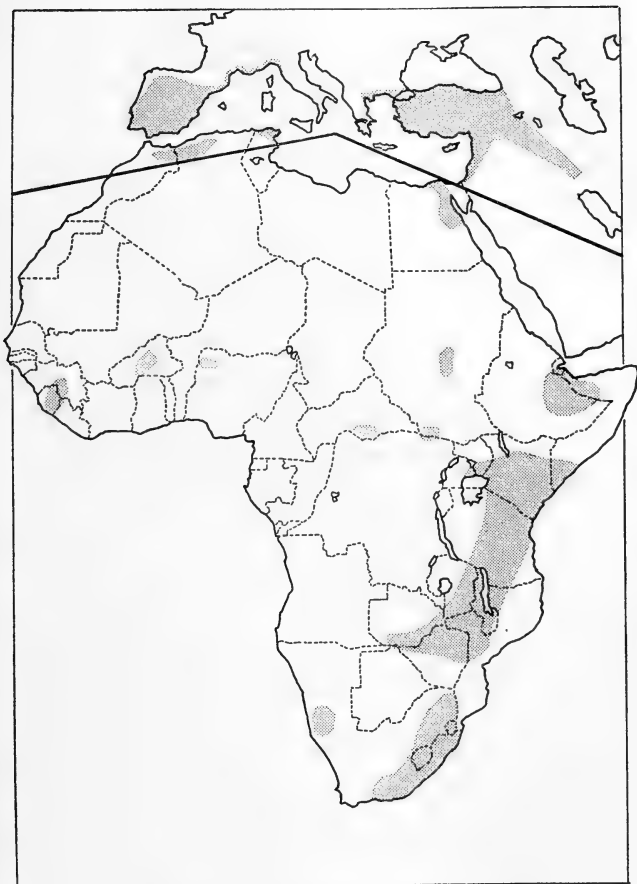


FIG. 7.—Known breeding range of *Clamator glandarius*.
Area of sympatry with *Pica* lies north of heavy line.

Eudynamis scolopacea, in northern India, may have influenced the eastward emigration of early *glandarius* to areas free from such difficulties.

The close resemblance between the eggs of the great-spotted cuckoo and of the magpie is evidence of a long continued and very specialized host-parasite relationship. As Baker (1942, p. 85) wrote, the parasite lays, "... one type of egg and one type only which is so exactly like in colour, shape, and superficial appearance of texture to that of the Magpie that identification is generally extremely difficult" It may be stressed at this time that the egg, speckled with dusky, is a highly "advanced" egg type for a cuckoo, the basic, primitive egg type in the family being unmarked white, and it has arrived long ago at a stage far beyond the development evinced in any other species of *Clamator*. That it is "fixed" and invariable, and that it now persists unchanged in the vast stretches of sub-Saharan Africa, where it does not match the eggs of the hosts used there, is evidence for the age and the finality of this "end product" of adaptive evolution.

If we were to assume, without documentation, as Voous (1960, p. 154) has done, that *C. glandarius* originated in sub-Saharan Africa and hence, that it there evolved its egg type in the absence of any known host whose eggs it resembled, and then later invaded Mediterranean Africa and the Iberian Peninsula, where its eggs "fitted" so well with those of the magpie, we would have a most remarkable example of extreme preadaptation. It would be so remarkable that it would be difficult to accept it without extremely disturbing doubts and skepticism.

If, on the other hand, it be accepted, as here postulated, that *Clamator glandarius*, having arrived at a perfected stage of adaptive evolution with regard to the degree of similarity of its eggs to those of the magpie, its chief, and almost its only, host in Asia Minor, in the Iberian Peninsula, and in northwestern Africa, then expanded its range southward into areas where this adaptive excellence no longer had its former value, we would have a case of what may be called "repudiative evolution." Part of the species acted as though the matter of egg resemblance no longer mattered, and in its new home used new fosterers to which it was not adapted. In a sense, this amounted to an escape from too specialized a form of host relationship; one which, had it been adhered to, would have markedly limited the parasite geographically, for the cuckoo is a bird of warm climes, whereas the magpie's range extends far to the north where the parasite would not be able to follow it, and the two are sympatric only in a limited area.

The importance of settling the question as to whether *glandarius* was originally sub-Saharan in range and later spread to the Mediterranean areas, or vice-versa, warrants a little further discussion. Voous (1960, p. 154), the only proponent of an African origin for the species, considered the hypothesis for such an origin "... supported by the occurrence of at least three other species of the genus *Clamator* in Africa . . ." This is incorrect as there are only two, *jacobinus* and *levaillantii*, while in Asia there are also two, *jacobinus* and *coromandus*. The last named is the species to which *glandarius* is most clearly related and appears to be the stock from which it arose. During a visit to Los Angeles in 1962, Stresemann, who has been studying very carefully the distributional history of the birds of Europe, agreed with me in considering the sub-Saharan range of *glandarius* as a recent expansion from an older circum-Mediterranean one.

In this connection we may recall, in Dobzhansky's (1940, pp. 312-321) words, that "... each species, genus and probably each geographical race is an adaptive complex which fits into an ecological niche somewhat distinct from those occupied by other species, genera, and races. The adaptive value of such a complex is determined not by a single or a few genes, but is a property of the genotype as a whole. Furthermore, the adaptive complex is attuned to its environment only so long as its historically evolved pattern remains, within limits, intact . . ." *Clamator glandarius* is highly adapted to the magpie, but yet part of its population has been able to abandon this evolved situation and to become attached to as different a host relationship as that with *Spreo bicolor* in South Africa.

One cannot help but wonder if this exodus of part of the Mediterranean *glandarius* may have been influenced, if not caused, by intra-specific competition in a too populous stock of the species, after its adaptive evolution had seemingly expedited its existence. Haldane (1932, p. 119) pointed out that there is a fallacy in the concept that "... natural selection will always make an organism fitter in its struggle with the environment. This is clearly true when we consider the members of a rare and scattered species. It is only engaged in competing with other species, and in defending itself against inorganic nature. But as soon as a species becomes fairly dense matters are entirely different. Its members inevitably begin to compete with one another . . ."

Inasmuch as the other three species of *Clamator* parasitize almost exclusively birds that build open, "saucer-shaped" nests, it may be assumed that a similar host choice is, or originally was, basic in *glandarius* as well, and that the use of hole-nesting starlings is a

relatively recent development. The surprising thing is not only that it was able to make this change, but that it had previously gone so far in the road of adaptive specialization to a host with which its area of sympatry was so limited.

The magpie genus *Pica* occurs throughout Europe, including the Mediterranean islands, and Asia north of the tropics (*i.e.*, north of the Arabian Peninsula, Baluchistan, Pakistan, India, Burma, Assam, and the Malayan countries), east to the western part of North America, and south from Gibraltar to northwestern Africa (Morocco, Tunisia, Algeria). In all the vast extent of this primarily Holarctic range, it is sympatric with its "highly adapted" brood parasite, *Clamator glandarius*, only in the Iberian Peninsula, adjacent portions of northwestern Africa (Morocco, Tunisia, Algeria), parts of southeastern Europe, Cyprus, and the Near East as far as Iran. This area of sympatry is thus a somewhat peripheral part of the range, both of *Pica* and of *Clamator glandarius* (whose geographically most extensive range is African south of the Sahara all the way to the Cape, and in eastern Egypt). An instance of the degree of sympatry of *C. glandarius* and *Pica* in southwestern Europe is the absence of both from the Balearic Islands although both occur in the Iberian Peninsula and in Morocco.

If the egg coloration of *Clamator glandarius* evolved to match that of *Pica*, this must have taken place in this limited area where the two occur together. The bulk of informed opinion regards the close egg resemblance as something arrived at by adaptive evolution, and not as a fortuitous coming together of a parasite and a host whose eggshells were similar in color, pattern, and size. The latter interpretation would assume an improbable and unlikely happening, although it cannot be ruled out as a possible explanation. The fact that throughout its range, the great-spotted cuckoo lays only this one type of egg suggests that its original range was just those areas where its egg type was adapted to a prevalent host. This further suggests that the *Pica*-allopatric portions of its present range in Egypt and in Africa south of the Sahara must have been a more recent extension of its distribution.

Amadon (1947) ascribed a marked change of bill form and of feeding habits in a Hawaiian honeycreeper, genus *Hemignathus*, to a sudden ecological shift of its ancestral population. Mayr (1959, pp. 177-178) considered that such a shift into an entirely new ecological niche may well have been the type of occasion attendant upon the emergence of many major evolutionary novelties. When

Clamator glandarius extended its breeding range into sub-Saharan Africa, the ecological shift was one that involved a marked change in host choice, even a virtual repudiation of a previously highly evolved egg adaptation, but, as it did not involve any apparent, drastic alteration in the daily life or feeding habits of the adult cuckoo, no comparable evolutionary change transpired.

It follows from this that, whereas in the case of self-breeding birds the entire biology of the species is a closely coordinated unit (almost what in current commercial jargon is referred to as a "package deal") on which selection may operate, in the case of brood parasites there is cleavage resulting in two fairly separate parts. The evolutionary climate ambient to the egg and nestling stages is that of the host species and has relatively minor connections with, and repercussions upon, the selective factors surrounding the life of the adult parasite. This may have helped make it possible for *Clamator glandarius* to invade vast new areas and to remain unchanged. Concurrently, it must be assumed that the new, non-egg-adapted hosts, suddenly parasitized by the newcomer, had no previous need to evolve any particular acuity of discrimination and thus were relatively easily susceptible to parasitism.

As far as casual observations go (and these are all that have been recorded in the literature), the great-spotted cuckoo seems equally successful in the various portions of its range. It might be expected that the wide discrepancy in the degree of host adaptation it shows in tropical and southern Africa on the one hand, and in the Mediterranean area on the other, would be reflected in its local numerical status, but the available evidence does not point to any such effect. It must be admitted, however, that the data are still very superficial and imperfect. If anything, the fact that unusually large numbers of its eggs are often found in single nests of its corvine hosts in the areas where the cuckoo is nonadapted might even suggest a relatively greater abundance of the parasite in proportion to the available host population there.

The known hosts of the great-spotted cuckoo, as listed here, are primarily birds of two families, the Corvidae (crows, jays, magpies, and piapiacs) and the Sturnidae (starlings). The other three included species are a kestrel, which was probably an "unintended" host choice as the bird was using an old magpie nest, and two South African ground-tunnel nesters, the hoopoe and the ground woodpecker, which may have been "acceptable" to the parasite because of

their general similarity to the nesting tunnels of the pied starling, *Spreo bicolor*, a favored and frequent host there.

The predominant role played by members of the Corvidae as fosterers of this cuckoo is indicated by the fact that of a total of 172 nests parasitized, 141 were of various corvids; 89 nests belonged to crows of 6 species (*Corvus corax*, *corone*, *ruficollis*, *albus*, *rhypidurus*, and *capensis*); 1 was of a raven, *Corvultur albicollis*, 48 were of 2 species of magpies (*Pica pica* and *Cyanopica cyanus*), 1 was of a piapiac (*Ptilostomus afer*), and 2 were of a species of jay (*Garrulus glandarius*). Of the remaining 31 parasitized nests, 28 belonged to 7 species of starlings. Of these 14 were of the pied starling, *Spreo bicolor*; 5 of the red-winged starling, *Onychognathus morio*; 4 of the glossy starling, *Lamprotornis nitens*; while of the other species single instances only have been reported so far.

Falco tinnunculus tinnunculus (in an old <i>Pica</i> nest)	Pica pica bactriana
Upupa epops africana	Pica pica galliae
Geocolaptes olivaceus	Pica pica melanotos
Corvus corone sardonius	Pica pica mauritanica
Corvus corone corone	Garrulus glandarius krynicki
Corvus ruficollis edithae	Ptilostomus afer
Corvus corax corax	Acridotheres tristis tristis
Corvus albus	Onychognathus morio morio
Corvus capensis capensis	Spreo bicolor
Corvus capensis kordofanicus	Spreo albicapillus
Corvus rhypidurus	Lamprotornis nitens phoenicopterus
Corvultur albicollis	Lamprotornis caudatus
Cyanopica cyanus cooki	Lamprotornis chalybeus cyaniventris
Pica pica pica	Lamprotornis chalybeus sycobius

As we have seen in the case of *Clamator jacobinus*, in the present species also, it is the sub-Saharan segment of its total membership that is the less well adapted in its egg coloration. However, in both these species, the available observational evidence gives no grounds for assuming that the sub-Saharan birds are less "successful" than their more completely and more perfectly adapted northern segments, insofar as "success" may be implied from ability to survive in numbers over a vast area.

We cannot, however, deduce from this that adaptation has lost its value and significance in one geographic portion of the total distributional range of this one genus of birds, while remaining advantageous elsewhere in the same genus, as well as in most of the rest of the animal kingdom. Certainly the case for the natural selective value of adaptation generally is so strong, so well-nigh invariable, that we

cannot easily accept its apparent unimportance here. At least part of the answer to this puzzle lies in the fact that because these two cuckoos were studied earlier in India and in the Mediterranean lands than in sub-Saharan Africa we have come to accept the adaptive excellence reported for them from those areas as an essential and necessary aspect of their natural economy. But now we know that, advantageous as this may be, it is not essential, and that the two species can and do survive without it. Actually, this is implied even in the course of the evolution of the climax adaptation in the areas where it has transpired, as countless less completely adapted generations had to survive to provide the material out of which was achieved the greater perfection, which in time supplanted the less adapted birds.

We have, then, a superficially similar situation in southern Africa in both the great-spotted and the jacobin cuckoos, but one which appears, on more careful study, to be due to opposite evolutionary trends. In the jacobin it seems probable that the southern population, *serratus*, is the original, primitive segment of the species that has remained as it was while giving rise to the more advanced *pica* and *jacobinus*, an evolution involving primarily the change from unpigmented to pigmented eggshell. On the other hand, the fact that in sub-Saharan Africa *glandarius* is not only bereft of the adaptive advantage its egg evolution had given it in Mediterranean lands, but further that in its southern range there is a striking difference in the numerical relationship of parasite-host eggs in parasitized nests in the two areas causes the southern population of this species to seem relatively so inept that it may only be explained on the basis of the recency of its invasion into that area.

What has happened with *C. glandarius* is paralleled by a similar, though less extensive, move in the jacobin cuckoo. Although the geographic spread of *C. jacobinus* from Africa to India is something that happened relatively early in its evolutionary history, the species has expanded its range in India more recently by advancing higher into the hills. Thus, Baker (1942, p. 83) considered it possible that its present breeding in the hills up to 6,000 feet and even higher in Assam and in the central Himalayas was a "modern extension of its breeding habitat. In the Plains . . . its normal fosterer, or group of fosterers is so completely established that exceptions are very, very few. In the lower hills the Cuckoo adheres closely to the Necklaced and the Striated Laughing-Thrushes, but above the normal elevation of the breeding areas of these birds or

where these birds are not found, or are rare, it launches out into the use of all kinds of nests which bear some resemblance to those they usually cuckold . . .”

The timespan involved in the southward spread of *Clamator glandarius* to sub-Saharan Africa need not have been great. The case may well have been similar to the recent rapid, almost “explosive,” spread of the cattle egret, *Bubulcus ibis*. In both instances the advancing birds filled vacant ecological niches. The cattle egret had no competition from other herons because it was a dry land bird and lived largely on insects, not an aquatic feeder on fishes, tadpoles, etc. The great-spotted cuckoo was parasitic on corvids, a group until then unmolested by any parasitic birds in Africa. The spectacular spread of the collared turtle dove, *Streptopelia decaocto*, in Europe during the past 50 years is a parallel example.

It seems that the relatively recent, but very extensive, geographical expansion of *C. glandarius* originally was motivated by the bird rather than by its environment. This statement may require a little elaboration to make its meaning clear. Evolutionary changes are often the result of a double process of selection; selection by the environment of the most advantageous, best adapted structural, functional, or behavioral organization in the organism, and also selection by the animal of the most comfortable, the most nearly optimal environment. The capacity for making a choice among available environments is inherent in all animals that are able to move about freely. In effect, this results in a process of sorting out the members of a species environmentally instead of selectively eliminating the less fit in the original ecological situation.

Implied in the phrase “sorting out” is what appears to have been behind the great move to sub-Saharan Africa. The part of the original circum-Mediterranean population of *C. glandarius* that was relatively less completely “fit” was the part that moved on to new territory—in this case, to equatorial and southern Africa. That it was less delicately, or less nicely, adapted to its original hosts than was the part that stayed in the Mediterranean area is still evidenced by its lack of adjustment in its egg deposition to the size of the total resulting clutches in the nests of its victims. This significant difference in the two geographic segments of *C. glandarius* is discussed in detail in our account of the intensity of parasitism (see pp. 38-47), but a little additional comment seems called for here.

While it is obviously impossible to state precisely what factor, or factors, motivated the dispersal of part of the *glandarius* population

from its Mediterranean homelands, it seems likely that it was growing population pressure, such as we have seen recently in the case of the cattle egret, mentioned above. The latter bird had increased greatly in numbers in Africa prior to its sudden geographic advance. Coincident with a situation of overpopulation, it may be remembered that the nature and the intensity of natural selection varies with different degrees of abundance of a species. When a species is numerically uncommon the selection pressure it experiences is exerted chiefly by the environment, whereas when it is more abundant the selection is often between members of its own species. It was selection of the latter kind that seems to have been involved in the emigration of the less adapted members of the *glandarius* population.

The lack of any fine control in the intensity of parasitism, as evinced by multiple-egg deposition and the resulting uncorrelated egg complements in parasitized nests, in sub-Saharan *glandarius* is more than a matter of an as-yet-unachieved adaptation. It is also an indication that the cuckoo is a recent arrival and is increasing in numbers, because at a time when the size of the population of a species is growing, selection is usually relatively weak, and such excesses as extreme multiple parasitism would be tolerated, whereas in a stable, "climax" situation this would be less apt to succeed.

Conversely, selection is apt to be stronger when the population of a species is decreasing. This must have been the case in the Mediterranean *glandarius* when part of the species emigrated southward, thereby reducing the intraspecific competition and permitting a more active environmental selection. This may actually have contributed to the development of an even better controlled host-parasite relationship there. As Carter (1954, p. 255) has stated, ". . . the population that survives the decrease of numbers will be a selected, and not a random, sample of that at the preceding maximum. Only the better adapted are likely to survive . . . It follows from this that adaptive evolution will be accelerated at the time of decrease . . ."

As the great-spotted cuckoo extended its range into sub-Saharan Africa, where there were no magpies, it undoubtedly used at first the nests of various species of crows for its egg laying, just as it had already done in eastern Egypt and the Near East. However, while it continued to use the arboreal nests of corvine hosts throughout its new domain it also extended its host choice to include such very different types of nest structures as those of an earth-tunneling starling, *Spreo bicolor*. It is known that in some animals specific types of nest structure may act as isolating mechanisms, preventing

mismating. So marked a change as that between the arboreal, bulky nests of masses of twigs and sticks of the magpies and crows, and the terrestrial nesting tunnels of the pied starling might seem more than sufficient to have functioned in its impact on the behavioral patterns of the cuckoos in much the same manner as an isolating mechanism. However, the differences involved, real as they are to human eyes, did not appear to affect the parasite.

In this connection I may say that I have tried to find a place where both the pied starling and one or more species of crows were present in numbers as breeding birds and where the great-spotted cuckoo also bred, but have not been able to do so. Such a locality might give an observer the opportunity to study the host choice of the parasite where both types of hosts were equally available.

The matter of host nest selection appears to affect the life and activities of the cuckoos only during the brief moments of actual ovulation by the hens. It may be remembered that mating or copulation by the cuckoos does not take place in or at the nests of any of the hosts, and that the cock cuckoos do not necessarily even know which nests receive the eggs they may have fertilized.

While the difference between the two extreme types of egg depositories used—the open, dish-shaped, arboreal, stick nest of a crow and the long earth-tunnel of a pied starling—are great, the change probably was not as abrupt as it might seem. To begin with, the host to which the great-spotted cuckoo's evolution has made it most adequately adapted is the magpie, a bird which customarily makes large nests of small branches, twigs, and sticks, roofed over, with an entrance on one side, and usually constructed in large thorny bushes or on the upper branches of tall trees. From this it was not a great change for the parasite to use nests of the crow in eastern Egypt and the Near East, the chief difference being that the nests of the latter were open, not roofed over, but were constructed of similar materials and in generally similar types of situations. From one species of crow to another (from *C. corone* in Egypt, Iraq, etc., to *C. albus* and others in sub-Saharan Africa) involved no vital change for the parasite, but the change from these to hole-nesting starlings seems quite marked. However, even this was neither abrupt nor as drastic as one might assume. In former British Somaliland (now a part of the Somali Republic), a somewhat intermediate stage has been reported by Archer (1961, in Archer and Godman, pp. 649-659). He found several eggs of the great-spotted cuckoo in nests of the white-capped starling, *Spreo albicapillus*, a species that builds bulky,

domed nests of twigs and coarse grasses high up in trees—nests quite similar in their main features to those of the magpies, the parasites' primary fosterers. From laying eggs in these domed, internally dusky, if not dark, somewhat tunnellike egg chambers of *Spreo albicollis* it was not a great step to using the darker nests of true tree-hole nesters, of other species of starlings, such as *Lamprocolius nitens* and *L. caudatus* and *Acridotheres tristis*. More of a change was involved in the shift from these to terrestrial burrowing hosts such as *Spreo bicolor*, but even here there may have been a transition stage, as this starling is said to nest in a variety of sites such as are used by *Sturnus vulgaris* as well as in its more usual earth burrow. Priest (1948, p. 118) indicated that this variety of nesting sites includes crevices on walls, under the eaves of houses, in trees, as well as breeding in tunnels in soft river banks or cuttings, or in mine shafts. I am informed by Dr. Winterbottom that the nest record files of the Percy Fitzpatrick Institute of African Ornithology extend this list of sites to include haystacks and even a crevice of a concrete platform in the sea (obviously near shore).

Once the cuckoo had become used to the pied starling as a fosterer, it could be expected to be attracted to it regardless of just where the nest was built. From terrestrial burrow nest-sites of this starling it was no great change to utilizing other similar nests, such as that of the ground woodpecker, *Geocolaptes olivaceus*. The pied starling is the most frequently used host in eastern South Africa today.

A partial parallel to what transpired in *Clamator glandarius*, as outlined above, has also been reported occasionally for the Indian koel, *Eudynamis scolopacea*, a cuckoo parasitic also very largely, in fact almost solely, on crows. Baker (1942, p. 197) listed two starlings, *Acridotheres tristis* and *Graculipica nigracollis*, among its known hosts, the former one or two times, the latter more often. However, as far as known, the koel has not adapted itself to terrestrial-nesting hosts. Baker listed 209 eggs of the koel in his collection. Of these, 16 were laid in nests of the black-necked mynah, *Graculipica nigracollis*, 2 were with *Acridotheres tristis*, 6 in nests of 2 species of magpies, and the other 185 in nests of 2 species of crows.

Even the European cuckoo, *Cuculus canorus*, has been known to lay occasionally in the underground nests of the wheatear, *Oenanthe oenanthe*. Furthermore, and more directly pertinent, it may be recalled that one egg of *Clamator jacobinus* has been reported from a ground-tunnel nest of a kingfisher, *Halcyon a. albiventris*, and another from a tree-hole nest of a sparrow, *Petronia supercilialis*.

Also, *Clamator levaillantii* has been known to lay in the hole nest of a kakelaar, *Phoeniculus purpureus*. The tendency to utilize such nesting sites has certainly not developed in *jacobinus* to the extent it has in *glandarius*, but these instances show that it is not outside the range of possibilities even in the former.

One further thought emanating from a consideration of this problem of host selection may be added here. Recent studies on many species of self-breeding birds, particularly in North America and Europe, have shown that nest-site selection is fairly rigid and fixed in its major elements. Slight vegetational differences often are critical to various species in the precise location of their nest sites. So widespread is this tendency that it is only proper to apply it to a review of the situation in brood parasites as well. In these birds nest-site selection would be altered to host selection based on the types of nest-sites used by the latter, and would be expressed in terms of host specificity as far as the parasites are concerned. On the whole, avian brood parasites fall into three main categories in this respect. Some exhibit little or no such specificity; others are specific in their host choice as individuals only ("individual-host specificity," as found in the European cuckoo, *Cuculus canorus*); and in still other parasites the entire species is specific on one or a small group of related hosts ("species-host specificity").

Inasmuch as nest-site selection does reflect trenchant and remarkably uniform criteria in each species of self-breeding birds (potential hosts), and inasmuch as there is no reason to assume that parasitic species, especially early in their evolutionary history, were necessarily different from self-breeding birds in their response to familiar and uniform environmental details, it may be that species-host specificity, as opposed to individual-host specificity, was the original situation in brood parasites and that a broader range of host choice developed from it later. This would imply that the broad spectrum of hosts subsequently arrived at may have evolved even as a negation of the original selection pressure that operated in an earlier atmosphere of species-host specificity. From this concept it would follow that rigid, if not actually "obligate," parasite-host specialization is a basic rather than an ultimate condition. This is quite the reverse of the often assumed pattern of species-host specificity arising from individual-host specificity.

In this connection it may be pointed out that the one species of brood parasite whose descent from a self-breeding form is most obvious and clear, the screaming cowbird, *Molothrus rufoaxillaris*,

started with, and has not deviated from, a fixation upon a single-host species, its close and antecedent relative, the bay-winged cowbird, *M. badius*. Furthermore, the parasitic Viduinae are still in the original stage of limited range of hosts, their Estrildine relatives, the waxbills. It also seems not improbable that the great-spotted cuckoo, *Clamator glandarius*, early became involved with, and went through its eggshell evolution with a single host, the magpie, *Pica pica*; the same is true of the stripe-breasted cuckoo, *Clamator levaillantii*, with its chief host, the babbler, *Turdoides jardineii*, and of the koel, *Eudynamis scolopacea*, with its use of crows. The evolution of host egg similarity obviously is facilitated by species-host specificity.

INTENSITY OF PARASITISM

By intensity of parasitism two quite separate things are implied. The percentage of the total nests of frequently used hosts that are parasitized gives one aspect of the parasite-host situation. The frequency with which individual parasitized nests are found to contain more than one egg of the cuckoo adds still another element of the total picture. On the whole, increase in frequency of multiple-egg parasitism on the same pair of hosts is something that is superimposed on the basic situation. While in some areas where the host nests are very numerous the incidence of multiple parasitism appears to be lower than in places where there are relatively few hosts for the number of cuckoos, this cannot yet be demonstrated convincingly, as in no area have the data been sufficiently extensive and intensive to give a precise survey of the numerical status of the hosts and of the parasite, or of the percent of nests of the favorite fosterers that are parasitized. Perhaps the nearest approximation to the kind of information needed is that afforded by Mountfort (1958, p. 54). In his fieldwork in Spain, he examined 7 nests of the magpie on one afternoon and found that 5 of them were parasitized by the great-spotted cuckoo, an incidence of simultaneous parasitism of 71.4 percent in a circumscribed area. Mountfort did not list the numbers of eggs or of young of either the host or the parasite in each of these nests, so his observations tell us something of the percent of magpie nests parasitized but not how intensively they had been affected. However, a compilation of all the cases he mentioned shows that of eight parasitized nests, none were found to have only a single cuckoo egg apiece. His figures are quite different from those given below for 28 other parasitized magpie nests, all also from Spain. Mountfort found some 50 occupied magpie nests in that country in 1956, but

did not specify if the 8 parasitized ones that he discussed were the only ones so affected.

The lack of sufficiently comprehensive or detailed quantitative observational evidence makes it necessary, at least for the present, to rely on the available data on multiple parasitism of individual nests as our primary method of evaluating the host-parasite relations. Of all the species of *Clamator* the one that is most revealing of evolutionary change in this important regard is the great-spotted cuckoo, *C. glandarius*, and we may, therefore, begin with it. The data on this species are as follows.

Clamator glandarius

Of a total of 172 parasitized nests, containing 407 eggs of the cuckoo, 82 had a single one each, 41 had 2, 13 had 3, 13 had 4, 10 had 5, 5 had 6, 1 had 7, 4 had 8, 2 had 10, and 1 had 13. In other words, some 47 percent of the nests contained single eggs of the parasite. However, considering that the first cuckoo egg laid in a nest was a "single" one at that time, and counting only the subsequent eggs as "multiples," the total is 172 singles and 235 multiples. In other words, multiple eggs were almost 50 percent more frequent than singles. While this is a general condition, it does not give a representative picture of the situation as it really is in any one geographic fraction of the total range of the parasite.

To make the data more comparable, we may eliminate for the moment all cases involving hosts other than species of crows. Six species of the genus *Corvus* (*corone*, *corax*, *albus*, *capensis*, *ruficollis*, and *hippidurus*) are parasitized, and together account for more than half of all the records (fig. 8). Out of 43 parasitized crow nests found in Spain, Asia Minor, and Egypt (the bulk of the records are from Egypt) containing a total of 54 cuckoo eggs, we find that 33 nests had 1 each, 9 had 2, and 1 had 3. In other words, over 75 percent of the nests contained single eggs of the cuckoo, and, all in all, multiple eggs of the parasite were less than 25 percent as frequent as were singles.

Out of 35 parasitized crow nests from south of the Sahara—from former Italian Somaliland (now a part of the Somali Republic) to Nigeria and south to South Africa—only 5 had single cuckoo eggs, 7 had 2, 3 had 3, 6 had 4, 7 had 5, 2 had 6, 2 had 8, 2 had 10, and 1 had 13; a total of 148 cuckoo eggs for the 35 nests as compared with 54 eggs from 43 nests in the Mediterranean lands. In tropical and southern Africa less than 20 percent of the nests had single eggs

of the cuckoo, and, all in all, multiple eggs of the latter were three times more frequent than single ones.

In the Iberian Peninsula it is definitely established that crows are only infrequently parasitized and that magpies are the principal hosts. In Egypt, and in Africa south of the Sahara there are no magpies, and the various species of *Corvus* are regularly victimized. Judging

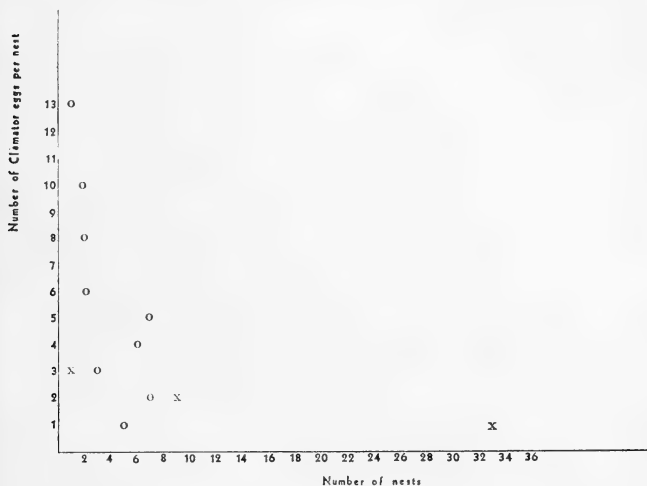


FIG. 8.—Frequency of multiple *Clamator* eggs in nests of *Corvus*.

O, In sub-Saharan Africa. X, In Mediterranean area.

from all the records available it appears that multiple eggs of the great-spotted cuckoo in Mediterranean lands are found more frequently in the nests of magpies than in those of crows. Thus, in Spain, Lilford (1866, p. 184) found a magpie nest with eight eggs of the cuckoo and five of the host, while Saunders (1869, p. 401) reported others with four and six cuckoo eggs in them, although he noted that other magpie nests had only one or two of the parasitic eggs apiece. As mentioned above, Mountfort (1958, pp. 54-56) found eight parasitized magpie nests in Spain. The number of eggs or young of the great-spotted cuckoo in these were as follows: One nest had six; two had five; two had three; and two had two.

In reply to my inquiry, J. D. Macdonald very kindly sent me the data on 28 parasitized sets of the magpie, all taken in Spain, and now

in the British Museum. In these the combinations of eggs of the parasite and of the host were as follows: 1 cuckoo egg in each of 10 nests with from 1 to 6 eggs of the magpie; 2 cuckoo eggs in each of 12 nests with from 2 to 8 of the magpie; 3 cuckoo eggs in each of 3 nests with from 1 to 3 of the magpie; and 4 cuckoo eggs in each of 3 nests with from 0 to 6 of the magpie.

Data are at hand on nine parasitized nests of the Spanish blue-winged magpie (*Cyanopica cyanus cooki*) from the Iberian Peninsula, *ex* Rey (1872, p. 143) and others, plus three sets in the British Museum; all of these had only single eggs of the cuckoo, with from one to five of the host. It is not possible, however, to say whether there is a significant difference in the intensity with which the two species of magpies are parasitized, although the available data appear to suggest that there may be. In both sets of data (*Pica pica* and *Cyanopica cyanus*), few of the sets approach the maximum size recorded for complete, unparasitized clutches—up to eight or nine eggs of either of the magpies. It can only be conjectured if this may have been due to elimination of host eggs by the parasite.

However, in the total count of instances of all host species, the recorded numbers of eggs of the fosterers in the individual nests do not consistently follow any variation directly proportional to the number of parasitic eggs found with them. We may recall that in his discussion of the great-spotted cuckoo as a parasite on species of magpies and of crows, birds larger than itself, Lack (1947, p. 323) reasoned that it might “. . . be anticipated that the host could raise more young than a single Cuckoo, and in fact, the young *Clamator* does not eject the members of the host brood, which are raised with it. However, the argument of this paper is that the full clutch of the Corvid host is determined by the average maximum number of young which the parents can successfully raise, hence even one additional nestling should upset the balance. It is therefore interesting that, according to Baker (1942) and Jourdain (*in* Witherby, et al., 1938-41) the parent *Clamator* removes one egg of the host species. Jourdain states further that a *Clamator* sometimes lays more than one egg in the same nest, in which case it is thought to remove one host egg for each egg of its own.”

Jourdain (1925, p. 657) did expressly state that the female great-spotted cuckoo usually removes an egg of the fosterer when laying one of her own, but in a later paper (1936, p. 739) he further wrote that “. . . in some cases the eggs of the Magpies are removed by the Cuckoos, for on one occasion I met with a Magpie's nest containing

four eggs of the Cuckoo but none of her own. Occasionally a Magpie manages to keep her clutch apparently intact, though unable to prevent the Cuckoos from depositing an egg or two. Thus, one bird was flushed from a nest with ten eggs, eight of her own and a couple of Cuckoos' eggs . . ." It seems from this that Jourdain's evidence was not unvarying, but still pointed to regular egg removal. Mountfort (1958, pp. 54-56) has added more evidence in support of this habit. He marked with indelible ink all the eggs in a number of parasitized magpie nests. ". . . The notes made subsequently at these nests . . . proved clearly that not only as many as three different hen cuckoos were laying in one Magpie's nest but that, as more eggs were laid, so the number of the host's eggs diminished. Moreover, on at least two occasions the addition of one Great Spotted Cuckoo's egg coincided with the disappearance of *two* Magpie's eggs . . ."

The picture revealed by the present data may be viewed graphically in figures 9, 10, and 11, in each of which is shown the distribution of the actual records, the number of instances of each particular combination of egg numbers being indicated in the graphs. By contrast, to emphasize the scattering, uncorrelated nature of this distribution, the dotted line represents the theoretical arrangements we should expect ideally from Lack's postulated clutch-size relationship.

All cases falling to the left, or below, the dotted diagonal line can only be interpreted as in agreement with the Lack relationship, as they represent clutches of eggs either collected or observed, but in all cases it is not only possible, but even probable, that had they been watched for subsequent days they would have had more eggs of either the host or of the parasite, or both, and would thus have moved closer to the line. The cases above and to the right of the dotted line are instances of disagreement with the postulated relationship, and it is their frequency with relation to those that concur with the diagonal line, and the degree by which they exceed this relationship that indicates the lack of adjustment between the parasite and its hosts.

It may be noted that the great-spotted cuckoo is relatively well adjusted in the intensity of its parasitism to magpies (fig. 12), very well adjusted to crows in Mediterranean lands, especially in eastern Egypt, and quite obviously little or not at all adjusted to crows and starlings (fig. 13) in sub-Saharan Africa. Because of the historical accident by which this cuckoo came to be studied in Spain earlier and more extensively than elsewhere, we have come to think of it as primarily a parasite on magpies and, because of that, we are apt to

think of its use of other hosts almost as relatively unusual. This concept is, as we now know, erroneous. As a matter of fact, the parasitism of this species on the magpie is remarkable in two very

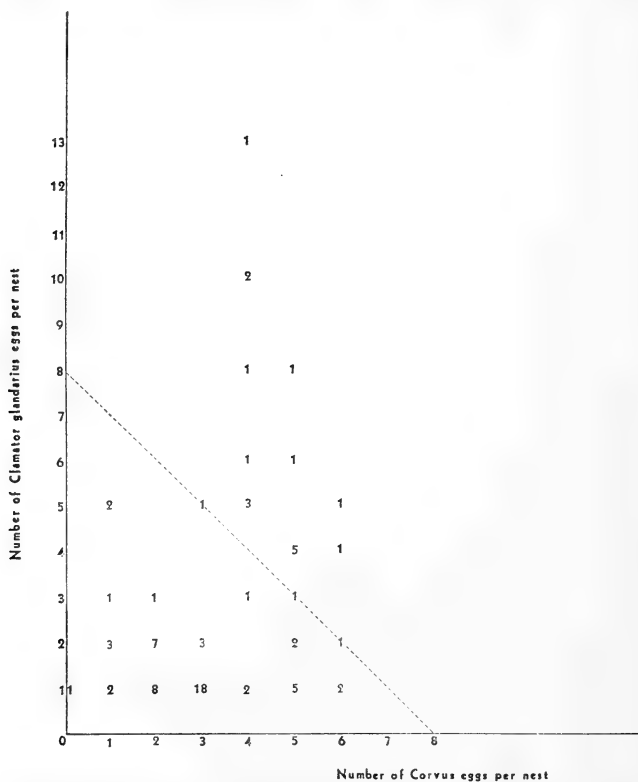


FIG. 9.—Distribution of *Clamator glandarius* eggs in nests of *Corvus*, and the number of instances of each particular combination of egg numbers.

dissimilar ways. For one thing, the adaptive resemblance in egg coloration between them is so close as to imply a lengthy evolutionary relationship between the two birds. On the other hand, at least in terms of their respective present distribution, the two are sympatric only in a very small, peripheral portion of the range of each.

A question that may arise from a perusal of this situation, and that merits some discussion is the following. It may be asked whether the striking difference in the degree of correlation between the egg numbers of the great-spotted cuckoo and of its hosts in the parasitized nests of the latter on the two sides of the Sahara might be explained by assuming that the sub-Saharan cuckoos do not have the habit of

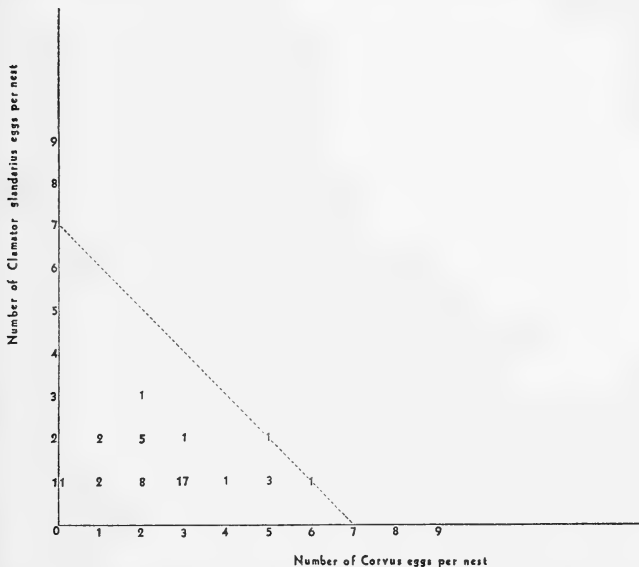


FIG. 10.—Distribution of *Clamator glandarius* eggs in *Corvus* nests in the Mediterranean area, and the number of instances of each particular combination of egg numbers.

removing one or more of the hosts' eggs when laying in the nest, as their Mediterranean counterparts are known to do. Against this explanation we may note that the egg-removing habit is also known in *C. jacobinus*, the most primitive member of the genus, and in *C. coromandus*, while lack of evidence on this habit in *C. levaillantii* cannot be looked upon as implying its absence. In other words, it appears to be a basic part of *Clamator* behavior, and it would be surprising if one population of the most advanced member of the genus no longer showed it. Furthermore, in numerous parasitized

nests of *Spreo bicolor* in South Africa, many of the hosts' eggs were found to be pecked prior to the hatching of the parasites, and hence this damage, comparable to egg removal, could only be attributed to

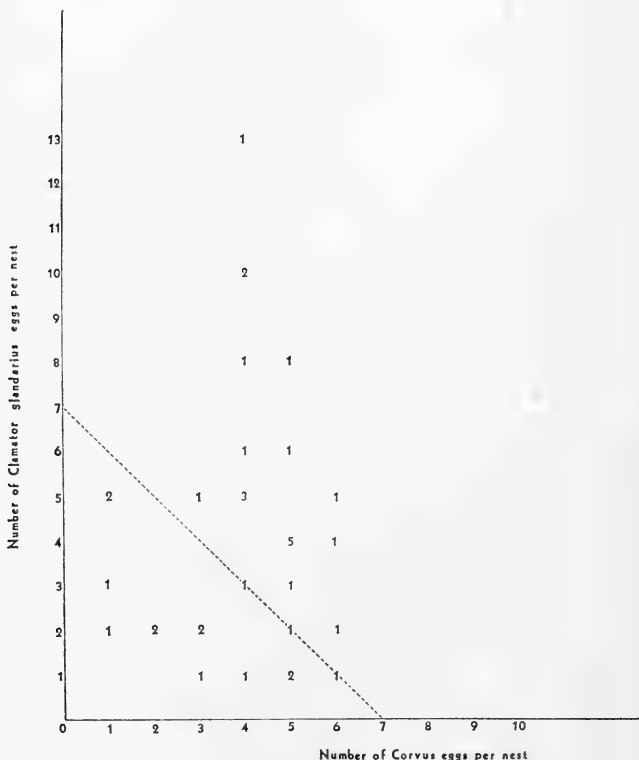


FIG. 11.—Distribution of *Clamator glandarius* eggs in *Corvus* nests in sub-Saharan Africa, and the number of instances of each particular combination of egg numbers.

the cuckoo. In the case of the long, narrow tunnels of the *Spreo* nesting sites it might be difficult for the parasite to remove the eggs, and pecking them may be a "substitute" behavior. To this extent it is evidence of the basic egg-removing habit in sub-Saharan *glandarius*.

Furthermore, out of 13 of the parasitized nests of the Cape rook, *Corvus capensis*, in southern Africa, described later in this paper (p. 99), 6 instances, containing a single cuckoo egg apiece, held from

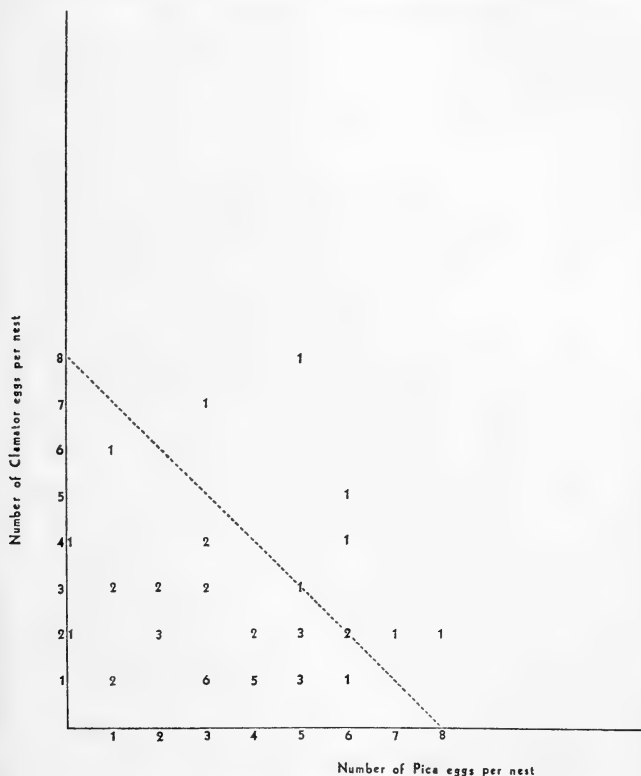


FIG. 12.—Intensity of *Clamator* parasitism to *Pica* indicated by number of instances of each particular combination of egg numbers.

1 to 4 eggs of the host, while in 7 nests with 2 cuckoo eggs apiece, there were from 1 to 3 eggs of the rook. This suggests at least a certain frequency of host egg removal, although it is true that other more intensively parasitized nests of the same species of host in southern Africa did not bear this out.

Recent knowledge gives us no reason for assuming any density dependent genetic factor that may operate in such a way as to control and to maintain a proper "spread" of multiple parasitism with reference to the resultant combined clutch size of the parasite and the

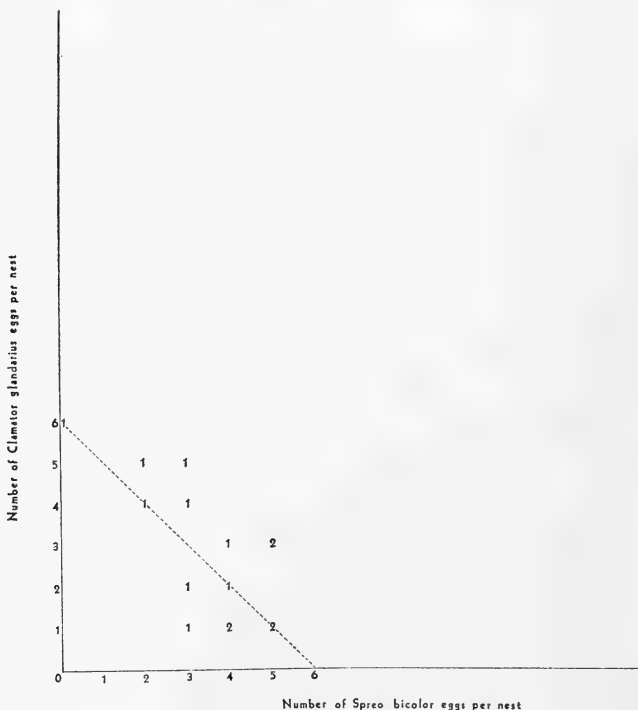


FIG. 13.—Intensity of *Clamator glandarius* parasitism to *Spreeo bicolor* indicated by number of instances of each particular combination of egg numbers.

host. Indeed, it is difficult to imagine just what such a factor or factors might be. The available evidence, incomplete as it is, suggests that it is not chiefly a matter of differential development of the habit of host egg removal by the parasite that is responsible for the striking difference we have found in the circum-Mediterranean and in the sub-Saharan populations of *Clamator glandarius*.

The high incidence of multiple eggs in *Clamator glandarius*, particularly in sub-Saharan Africa, raises the question as to the situation in the other members of the genus. A summary of all the available data gives the following figures, none of which comes up to those we have just considered.

Clamator coromandus

Baker's (1942, p. 152) data on 171 nests containing 225 eggs of this cuckoo reveal 171 were singles when laid, and 54, or 31.5 percent were multiples. Of the parasitized nests 139, or 81.3 percent had 1 cuckoo egg apiece, and 32, or 18.7 percent had been parasitized more than once.

Clamator jacobinus

Data on 220 nests containing 290 eggs of this species show 220 were singles when laid, and 70, or 24 percent, were multiples. Inasmuch as this is a species which has extended its range (from Africa to Asia) and is, in this regard, somewhat comparable to *C. glandarius*, we may treat the Asiatic separately from the African data.

Asia: 106 nests containing 142 eggs, of which 106 were singles when laid, and 36, or 25 percent, were multiples. Of the 106 nests parasitized, 84, or 78.2 percent, had but a single cuckoo egg each; 22, or 21.8 percent, had been parasitized more than once.

Africa: 114 parasitized nests were found containing 152 eggs, of which 114 were singles when laid, and 38, or 25 percent, were multiples. Of the 114 nests, 98, or 86 percent had a single cuckoo egg each, and 8, or 14 percent had been parasitized more than once.

We may point out that the absence of any significant difference in the ratio of multiple-egg deposition in the two great segments of this species is decidedly different from the comparable picture in the great-spotted cuckoo. It adds one more support to the contention that the great geographic spread of *glandarius* and of *jacobinus* were, in an evolutionary sense, quite opposite of each other. In the former species it was a very recent (late) advance after a high evolutionary development had been achieved; in the latter species it was an early spread prior to the evolution of egg adaptation. In *glandarius* the geographic "advancers" still reveal a lesser degree of efficiency in their host relationship than do their "stay-at-home" ancestors; in *jacobinus* this is not true. Of the total 220 nests parasitized by the latter species, throughout its range, 182 contained 1 egg each of the cuckoo, 21 had 2, 9 had 3, 5 had 4, 2 had 6, and 1 had 7.

Clamator levaillantii

Data on 23 nests containing 28 eggs of the stripe-breasted cuckoo reveal that 23 were singles when laid, and 5, or a little under 20 percent, were multiples. Of the 23 parasitized nests, 20, or 87 percent, had but a single cuckoo egg each, while 3, or 13 percent, had been parasitized more than once (2 had 2, and 1 had 4 cuckoo eggs).

Other Genera

A still higher incidence of multiple eggs is known to characterize the brood parasitism of another genus of cuckoos in southeastern Asia, the koel, *Eudynamis scolopacea*. This large, sexually dimorphic cuckoo is parasitic chiefly on crows, to the eggs of which its own show much resemblance. In its host selection it is, thus, comparable to *Clamator glandarius*. Baker (1942, p. 153) gives the following data on the koel, culled mainly from observations in India.

Out of 223 koel eggs laid in 93 parasitized crow nests, 93 were singles when laid, and 130, or a little over 58 percent were multiples. Of the 93 nests, 36, or 38.7 percent, held a single koel egg each; 57, or 61.3 percent, contained multiple eggs. The greatest number of parasitic eggs in any one nest was 16, but in 75 percent of the nests 1, or not more than 2, koel eggs were present; 8 nests had 3 koel eggs each, 7 had 4, 4 had 5, 1 each held 6, 7, 9, 11, and 16 koel eggs respectively. That Baker's data are not atypical is shown by many published observations on this cuckoo by others. Thus, to take only a single such note, Hopwood (1912, pp. 1211-1212) found koels to be unusually abundant at Arakan, Burma, and to be "wasteful" of their eggs. In one crow nest, apparently forsaken by its builder, he found seven koel eggs, which appeared to have been laid by at least three different individuals, and none of the crow.

In the European cuckoo, *Cuculus canorus*, by contrast, we find the birds almost always lays but one egg in a nest and it is relatively seldom that more than one hen uses the same nest. Thus, Baker listed 3,711 eggs of several races of this cuckoo in his collection, and from his various statements it is possible to estimate that in only 86 out of 3,617 parasitized nests were there more than a single cuckoo egg. To put it a different way, out of 3,711 eggs of *Cuculus canorus* 3,617 were singles when laid, and 94, or about 2.5 percent, were multiples.

While in *Cuculus canorus*, with its wide range of egg variability, it is possible to distinguish multiple eggs from the same hen, from eggs of multiple hens, this usually is not readily feasible in some species

of *Clamator*. Baker (1942, p. 152) has claimed otherwise, and he had behind him many years of experience, even if not of the most critical sort, when he wrote that "... several eggs of all the species of the genus *Clamator* ... may be found in the same nest, obviously the production of two or more Cuckoos ... For instance, in the set with six Pied Crested Cuckoos' eggs it is easy to see that they must have been laid, two each, by three different cuckoos ..." Yet, elsewhere in his work he stressed the fact that each species of *Clamator* lays a single, invariable egg type. The only variations that might be expected would be quite minor, and in many cases these would hardly suffice to distinguish the eggs of individual parents.

In the case of *C. glandarius* the greater variability of eggshell pattern makes it possible to distinguish between multiple eggs of the same hen and eggs of different individual cuckoos. Here there are acceptable records of more than one parasite laying in the same nest. Mountfort and Ferguson-Lees (1961, pp. 98-99) found as many as three cuckoos laying in single nests of magpies in Spain. What is true of *glandarius*, and, it seems, of *coromandus*, may or may not be true of *jacobinus* and *levaillantii*. There are not yet the necessary, careful observations to prove or to disprove this in these two species.

Because of this it is not profitable at this time to attempt to particularize our discussion of multiple parasitism in *Clamator* below the species level. In instances of maximal numbers of eggs in single nests it is highly probable that multiple hens were involved, but in cases of two, or even three, eggs in a nest, there is no certain way of telling.

Brood parasitism is a more precarious mode of reproduction than is self-breeding, as it involves all the risks normally attendant upon the nests it utilizes plus the elements of desertion of the nests or destruction of the eggs by the hosts. It is therefore plausible that any improvement, or any increased discrimination, in the matter of egg deposition would provide a basis on which natural selection would operate and, conversely, a basis from which the effects of such selection might be inferred. By and large, the chances of success for the parasite tend to decrease when more than a single egg is laid in the same nest. Many hosts may stand for a single imposition but not for repetitive ones without deserting the nest; others simply could not hatch and rear more than one or two of the parasitic young. It follows, therefore, that an original tendency to lay multiple eggs in the same nest would eventually be modified by natural selection, and that the relative frequency of such multiple eggs would tend to decrease in areas where selective pressure was in operation.

The situation we have just outlined in *Clamator glandarius*, especially in Africa south of the Sahara, and in *Eudynamis scolopacea* in southern Asia, appears, at first glance, to go counter to this idea. However, one important factor that enables their excessively multiple egg deposition to continue as a reasonably well-functioning habit is that both of them use large hosts, mostly birds as large as, or even larger than, themselves, that are capable of incubating successfully more of the eggs and of rearing more of the young of the cuckoos than is the case with other species of cuckoos, regularly parasitic on birds smaller than themselves. In the latter situation one cuckoo egg is often close to the limit of the hatching potential of the host, and in such cases multiple-egg deposition would merely bring about the loss of the nest and its contents. In other words, the fact that in the case of the great-spotted cuckoo and the koel the parasite-host size ratio tends to favor the host has the effect of lessening, if not eliminating, any selective pressure against multiple parasitism. This has made it possible for sub-Saharan *glandarius* to become established over a vast area. It seems, however, that as the frequency with which it selects smaller birds, such as starlings instead of crows, as fosterers increases, it will again be committing itself to the selective pressure to which it is temporarily fairly immune.

EGG MORPHISM

The great development of egg morphism in *Cuculus canorus*, with its connotations of adaptive evolution, could only have come about from a basic wide range of original variations in eggshell coloration. However, this is a highly specialized species, far removed from the situation in the crested cuckoos of the genus *Clamator*. In fact, the very simplicity of the whole matter of eggshell coloration in *Clamator* permits some suggestive glimpses into the early stages of a process that has not gone far in this genus, but that has not only advanced, but, in doing so, has obscured its past history, in *Cuculus*.

The basic, primitive, unspecialized type of eggshell in the cuckoos, as a family, is unpigmented, unmarked white. In this character the cuckoos agree with the doves, the parrots, the owls, the touracos, and also with the bulk of the scansorial and picarian families. The eggs of the relatively unchanged, nonparasitic cuckoos are either plain white or tinged with plain, unmarked, pale bluish, and this may be looked upon as the original, basic type in all cuckoos. However, numerous kinds of cuckoos lay eggs that are pigmented in a plain, overall tone, and, in the most highly specialized species, we find some

that lay eggs that are patterned, speckled, or blotched as well. The situation in the species of *Clamator* is discussed below in detail for each of the four forms, but in general it may be said that each species has but a single egg type, except for *C. jacobinus*, where we find two types, but which are geographically distinct, so that even there, in any one area there is but a single type. In *C. levaillantii* there is some, as yet not wholly satisfactory, evidence for incipient egg morphism; in *C. coromandus* and in *C. glandarius*, only one type apiece occurs.

Clamator jacobinus

So evident does it seem that uniform white is the primitive egg-shell type that I am influenced by it in considering the southeast African (*serratus*) population of *C. jacobinus*, with its pure white eggs, as the old, primitive portion of that species, and its other two races, *pica* and *jacobinus*, with their pale greenish-blue eggs, as more advanced. There is no other character that lends itself to judging their relative phylogenetic positions. In all the great number of eggs of this cuckoo taken in Ethiopia, the Somali Republic, Uganda, most of Kenya, and in India, not a single one has been found that was not plain, greenish blue. One white egg, taken from the oviduct of a collected female, was reported from Doinyo Narok, in southern Kenya, by Jackson (1938, pp. 495-496). One other white-shelled oviduct egg obtained near Timbuctu in Mali (formerly part of French Equatorial Africa) by Paludan (1936, p. 292). In an earlier study (1949a, p. 20) I suggested that the white color of this particular egg might have been due to the fact that it was "unfinished," an oviduct egg not quite ready to be laid, and that it might have been about to receive some bluish pigment. This has been countered by the results of Harrison's recent study (1963, pp. 154-155), which show that the pigment is distributed throughout the thickness of the whole shell in bluish eggs of this cuckoo. The example from Timbuctu, therefore, must be looked upon as a definitely white egg. The white Doinyo Narok example appears to have been even closer to laying time when collected. These two are puzzling records that cannot be "explained away" easily. The Doinyo Narok one is separated from the nearest (more southern) record of a pure white *jacobinus* egg by over 600 miles, the closest ones being from Nyasaland! It may be mentioned that the species has not yet been found to breed in Tanganyika or in the northern half of Mozambique, so there are no records of blue eggs between Doinyo Narok and Nyasaland either. The Timbuctu specimen is even more remote from known white eggs

of the species. Blue eggs are known from near Nairobi (Ngong), not too far to the north of Doinyo Narok. Clancey (1960, p. 29) has identified a breeding male specimen of the cuckoo from Lake Magadi, quite close to Doinyo Narok, as of the subspecies *pica*, a race whose eggs are bluish.

In South Africa, South-West Africa, Bechuanaland, the Rhodesias, southern Mozambique, and Nyasaland, the known eggs (and there are many) are pure white, except for one blue oviduct egg from Bulaya, 8°33'S., 30°07'E., near Lake Mweru, in northeastern Northern Rhodesia. It is possible that the local race of the cuckoo there is *pica* and not *serratus*, as it cannot be said, on present evidence, that *pica* may not be the breeding form of Ruanda-Urundi (now the Republic of Ruanda and the Kingdom of Burundi) and the eastern part of the Republic of the Congo near Lake Tanganyika, and that its range may extend south to Bulaya. On the map of the breeding ranges of the races of this cuckoo the egg color has been indicated, B for blue, W for white.

Several recent authors have considered *pica* inseparable from *serratus*, but while close I prefer to keep them distinct, as did Clancey (1960). As far as our immediate problem is concerned the only difference is that if they were merged we would have two egg types in one race, although geographically separate from each other, whereas in our present arrangement, each race has one egg type, but still the species has two. Inasmuch as *C. jacobinus* is the only species of the genus that has developed two distinct, and constant, egg types, it may be pointed out that the more "advanced" of the two, the pigmented, or greenish-blue, type is apparently the type developed in the stock that gave rise to *C. levaillantii* and to *C. coromandus*, both of which lay similar, unmarked bluish or bluish-green eggs.

The origin of two egg types, or, more precisely, the advent of the pigmented one in a species originally laying only unpigmented white eggs, is a problem for the solution of which no real clues exist, although we have already noted that nonparasitic cuckoos lay eggs that are either white or bluish white, and that there may be a tendency in the basic, primordial cuculine stock as a whole to produce some blue eggshell coloring. However, a parallel case has recently been described in a totally unrelated, primitive parasitic cuckoo, the Neotropical *Tapera naevia*. This bird, parasitic primarily on furnariids and dendrocolaptids, all of which lay white eggs, was known to lay white eggs as well. Haverschmidt (1961, pp. 353-359) has found, in Surinam, that this cuckoo lays two types of eggs, both unmarked,

one white, the other bluish green. Of 13 eggs taken near Paramaribo, 6 were white, 6 were bluish green, and 1 was white with a bluish tinge. In other words, in *Tapera naevia* we have a comparable trend, but without geographic separation of the two types as in *Clamator jacobinus*. Other examples, among nonparasitic birds, of two such egg types sympatrically, are *Diplootocus moussieri* and *Phoenicurus ochrurus gibraltariensis*, (Etchecopar, 1942). In this connection it may be noted that Etchecopar (1946, p. 160) suggested that the blue egg color might be a result of the greater humidity in the more tropical areas. He cited no evidence in support of this notion, and, indeed, it is not clear that the more equatorial birds do experience more humidity than do their more austral relatives. It is not clear just what he had in mind when he referred to the ". . . grande facilité la coquille à se tacher sous l'influence d l'humidite, il nait alors de grandes macules bleu fonce tres particulieres a ces oeufs. . . ." The blue eggs are not blue spotted; they are uniform in their blue coloration.

Clamator levaillantii

The eggs of the stripe-breasted cuckoo are uniform, glossy, pale bluish to greenish blue, somewhat pitted, and average 26×20.4 mm. Most of the recorded eggs are of this type, but there is evidence of some egg morphism in this species. Pale pink eggs, finely and faintly speckled with slightly darker pink, attributed with strong presumptive evidence to this cuckoo, have been taken in two nests at Kafanchan, Northern Nigeria, by Serle (1939, p. 689) and at Balgowan, Natal, by Bell-Marley (Friedmann, 1949a, pp. 44-45). Searle was of the opinion that the pink eggs were an adaptation to the similarly pinkish eggs of the local fosterer in Nigeria, *Turdoides plebeja*; no such seeming adaptation was involved in the Natal records, where the host (two cases) was the Cape robin chat, whose eggs were not pinkish, but pale greenish blue flecked with brown. It is true that in some instances the eggs of this bird are almost covered with light salmon-pink flecks.

To these two egg types we may add that it has been suggested in print that this cuckoo may occasionally lay pure white eggs. The evidence, if it may so be termed, is far from conclusive, but the case may be given here. Milstein (1954, pp. 4-5) observed two *Clamator levaillantii* showing much interest in a yellow-vented bulbul's nest. They repeatedly came toward the nest and each time were attacked by the bulbuls. The cuckoos, fluttering wildly, never at-

tempted to fight back, even when one of the bulbuls yanked out a tuft of whitish breast feathers from one of the intruders. Milstein watched this repeated series of attacks for over an hour and a half. Several hours later he returned and examined the nest which he found contained two eggs of the bulbul and four larger, pure white eggs of a cuckoo. One of the white eggs was on the rim of the nest, almost falling out; this one Milstein was inclined to assume had been laid by the stripe-breasted cuckoo during his absence. It was very slightly pinkish, which he interpreted as indicating extreme freshness. The white eggs measured 25.2 to 27 by 20.7 to 22.2 mm., agreeing with known eggs of both *levaillantii* and *jacobinus* in size, and with *jacobinus* eggs in color. If they were laid by *levaillantii*, they add a third egg type to the known range of its egg colors.

Clamator coromandus

The red-winged crested cuckoo lays but a single type of egg, uniform greenish bluish, slightly glossy, and averaging about 26.9 x 22.8 mm. According to Baker, who has studied it more extensively than anyone else, its eggs show good adaptive resemblance to those of its usual hosts, laughing-thrushes of the genus *Garrulax*.

Clamator glandarius

The great-spotted cuckoo also lays but one egg type, pale greenish white to pale greenish gray, abundantly spotted and flecked with fairly evenly distributed tiny dots and larger markings of various shades of yellowish brown, reddish brown, umber, grayish brown, and slate gray, many of the blotches with a pale lilac tone or under-marking. In many eggs the blotches tend to be more numerous toward the large pole and in some they almost fuse to form a ring there, but in others there is no such local concentration. In size they vary from 29.1 to 35.2 by 22.6 to 26.5 mm.

This is definitely an "advanced" egg pattern, more developed than the uniform ones of the other three species of *Clamator*. In a sense the pinkish eggs of *levaillantii* with their faint speckling of darker pink may be looked upon as foreshadowing the development that took place in *glandarius*. Makatsch (1955 pp. 218-220) has discussed the evolution of spotted from uniform egg coloration in cuckoos, and concluded, as I do, that these patterned eggs represent the climax stage, and not, as Baker and von Boxberger did, the early stage.

The eggs of the great-spotted cuckoo are smaller than those of its corvine hosts, although as large as, or larger than, those of its sturnid

fosterers. In the other species of *Clamator* their eggs are generally larger than those of their victims.

The egg pattern of the great-spotted cuckoo is so closely adapted to that of the magpie, its primary host in Spain, that it has often been mentioned as an example of perfected adaptive evolution. As we have had occasion to discuss elsewhere in this paper, there can be little doubt that it developed with the magpie as the chief host, and that the range of the cuckoo has subsequently been extended to areas outside the range of this fosterer.

As is so frequently the case, adaptations that seem, to the investigator, obviously functional, and, hence, readily understandable, suddenly seem to be unimportant and unnecessary when the organism possessing them moves into a different situation. In Portugal, and also in parts of Spain, the great-spotted cuckoo parasitizes the blue-winged magpie, *Cyanopica cyanus cooki*, and, in Egypt and in sub-Saharan Africa it uses even more divergent hosts. Etchecopar (1946, p. 165) admitted the striking similarity in the eggs of this parasite and those of *Pica pica*, but was moved to state that when the host was *Cyanopica* it was difficult to see any special resemblance (“... ou il est difficile de voir la moindre trace d'adaptation . . .”).

Recently Tomlinson (1962, p. 260) has stated that he found the great-spotted cuckoo parasitized the black crow (*Corvus capensis*) and the pied crow (*Corvus albus*) in South Africa, and that its eggs varied in color to match those of the host, pinkish in the case of *capensis*, greenish in *albus*! Fraser (1962, p. 343) and Calder (1962, p. 344) rightly questioned the identification of the pink “cuckoo” egg noted by Tomlinson. In the light of all we know at present there is no reason for thinking that the great-spotted cuckoo lays more than one type of egg. However, as I discussed in my earlier account (1949a, pp. 44-45) and in the description of egg morphism in *Clamator levaillantii* in the present paper, there are on record some four instances of pinkish eggs attributed with some presumptive evidence to the stripe-breasted cuckoo. In addition to these, Priest (1934, vol. 2, pp. 238, 245-247) reported a speckled, pinkish egg, supposedly of a cuckoo, in a nest of a pied crow (which lays greenish eggs that contrasted very strongly with it). He suggested that it might be either the stripe-breasted or the great-spotted cuckoo, and noted that its size, 29 x 23 mm., favored the latter identification. In discussing this record I suggested that it might have been a “runt” egg of the black crow; this suggestion would be even more appropriate in Tomlinson's record, as there the nest and the egg would both be identified to the same species.

The problem of egg morphism, is, as we have seen, not a prominent one in the genus *Clamator*. Still, by virtue of what it reveals in *Cuculus*, where it is well developed, it raises one further point that is worth discussing here. In the European *Cuculus canorus* we have a species with a wide range of eggshell coloration, and we have reasonably good evidence for the existence within the species of numbers of different gentes, each specific on a definite host species. The existence of two or more gentes sympatrically increases the efficiency of each in exploiting host egg mimicry, and allows a greater population of cuckoos to exist in a limited area. Regardless of the reality of these gentes, and no doubts as to their existence are here implied, it is true that the only way in which we may be made aware of them is by the fact that each individual hen cuckoo lays a single egg type, and is specific in its host choice, while the species lays a wide range of eggs and uses many species of hosts. From this it follows that if *Cuculus canorus* laid but a single type of egg it could still have gentes, but we would be unable to sense their existence and would have no reason even to conceive that there might be any. In the crested cuckoos of the genus *Clamator* we have seen that each species has but a single egg type, except for incipient variation in *levaillantii* and geographic variation in *jacobinus*. Consequently, no suggestion of gentes has ever been raised in studies of this genus, and, indeed there would seem to be nothing on which natural selection might have favored the development of such infraspecific categories. Still, we cannot rule out the possibility that the hens of each of the four species may be individually host specific (as in *glandarius* in the Iberian peninsula, where all the hens are essentially specific on the same host, the magpie). If this should prove to be the case, we would have, in effect, undistinguishable but yet actual gentes in the species of *Clamator*.

In this connection we may recall Southern's (1954, p. 223) conclusion about gentes in *Cuculus canorus* to the effect that those gentes which are highly adapted in egg mimicry probably thereby sacrifice a certain degree of what plasticity their ancestors may have had, and with it the ability to turn successfully to new and very different hosts. In effect, *Clamator glandarius* in the Iberian Peninsula and in adjacent parts of western Mediterranean Africa is comparable to a single highly specialized gens in *Cuculus canorus*. Yet it has been able to utilize remarkably dissimilar hosts in sub-Saharan Africa.

Whereas in *Cuculus* there is a definite trend for small egg size, relative to the size and weight of the adult bird, a trend which has

enabled the members of that genus to parasitize birds much smaller than themselves, no such reduction in relative egg size is found in *Clamator*. For that matter, diminution of egg size is found in all species of *Cuculus*, but not in other genera of parasitic cuckoos. Within the species *Clamator jacobinus* we do find a slight geographic reduction in egg size, but nothing comparable to the situation in *Cuculus*. The greenish-blue eggs of *C. j. pica* average slightly smaller than do the white ones of *C. j. serratus*, but the difference, while significant and, in an evolutionary sense, suggestive, is not trenchant as there is extensive overlap in the sizes of the two groups. Thus, eggs of southern African *serratus* vary from 24.1 to 28 by 20.8 to 23 mm., with an average of 25.5 by 22 mm.; while those of *pica* from Ethiopia vary from 22 to 25 by 20 to 22 mm., with an average of 23.5 by 20 mm., and eggs of *pica* from India range from 21.9 to 28 by 17.6 to 21.4 mm., with an average of 24.3 by 19.4 mm. The eggs of south Indian, nominate *jacobinus* are slightly smaller still, in keeping with the lesser size of the birds of that race.

The development of brood parasitism and the varying features it exhibits in different genera of cuckoos make it clear that each genus needs to be studied independently before we may attempt to generalize. In *Clamator* the evolutionary history of the egg size and coloration differs from that in *Cuculus*; it reveals no marked reduction in size and while it has achieved remarkable adaptive similarity to those of its hosts in color it has done this without developing any extensive egg morphism within any of its species.

INCUBATION PERIOD

Rapid development of the embryos, or shortening of the incubation period of the eggs, is generally considered as advantageous to a parasitic bird, as it may result in the parasite hatching before its nest-mates and thereby gaining a "start" on them. This would seem particularly pertinent to parasites that do not attempt to evict their nest-mates but grow up with them. If this concept were infallible we might expect to find a slight, but significant, change in this direction from the most primitive species of *Clamator*, the pied cuckoo, *C. jacobinus*, to the most advanced, the great-spotted cuckoo, *C. glandarius*. The few facts available, are, surprisingly enough, contrary to this postulated condition. The incubation period for *jacobinus*, as worked out carefully by Liversidge (1961, p. 624) in four instances, was between 11 days \pm 14 hours and 12 days \pm 12 hours, while in *glandarius*, Mountfort (1958, pp. 54-56) found it to be 14 days. As yet, no data are available on the other two species.

It should be kept in mind that even with its longer incubation of 14 days, *glandarius* averaged 3 to 4 days less in its incubation period than the magpie hosts it used in Spain, where Mountfort studied it. This would be true for its other corvine hosts as well. It may be that the greater size of *glandarius*, as compared with *jacobinus* is reflected in its longer incubation period, but this is by no means established. The incubation periods of the various hosts—shrikes, bulbuls, and babblers—that are used by *jacobinus* are shorter than those of the magpies and crows used by *glandarius*. It may be that the change in host choice in the latter offset any advantage that more rapid embryonic development might otherwise have given it.

HOST-PARASITE NESTLING RELATIONSHIPS

The development of brood parasitism in *Clamator* has not included the development of eviction by the newly hatched young.

In some parasitic cuckoos, notably those of the genus *Cuculus*, the newly hatched bird, while still featherless and with still unopened eyes, evicts from the nest in which it finds itself other nestlings and eggs. This it does by pushing against them and slowly burrowing under them until it gets them on its back, when it climbs slowly to the rim of the nest, where with a final and violent, muscular effort it heaves them out of the nest. Thereupon, it falls back into the nest, where it rests momentarily before tackling the next nestmate. This evicting behavior usually lasts only until the fourth day of life, after which the nestling cuckoo tolerates anything that may be in the nest with it.

This highly peculiar, and obviously instinctive, behavior is one of the features associated with brood parasitism that has not been developed by the species of *Clamator*. In *C. glandarius* and *C. coromandus* we have ample numbers of observations to be able to state that usually eviction by the newly hatched cuckoo does not take place. In *glandarius*, the elimination of the host young that often happens is due to their being either starved or smothered by their parasitic nestmates, and their dead bodies removed by their own parents. Thus, Mountfort (1958, pp. 54-56) wrote that in only one magpie nest in Spain did he find young of the host and of the great-spotted cuckoo together, and this was only for a very brief period, as the nestling magpie was gone 2 days later. It had hatched 3 days after the eggs of the parasite, and the emerging nestling was never able to overcome this disadvantage. Mountfort concluded that the shorter incubation period of the cuckoo (shorter by 3 days) doomed the young magpie,

and that only such young magpies as hatch from eggs laid well before those of the parasite can have any chance of surviving.

Similarly in South Africa, Miss M. Courtenay-Latimer (*in litt.*) watched a nest of a hoopoe, *Upupa e. africana*, that originally contained four eggs of the host and one of the parasite. The cuckoo egg hatched on the same day as the first host egg; the other three hoopoe eggs hatched on the following 2 days. The young hoopoes disappeared 3 days later, but their eviction or removal was not observed. The fact that they did not disappear until 3 days after hatching argues against eviction by the young cuckoo, and makes it appear likely that they perished in the matter of food competition with it.

Another case in point is one reported by Meyer (1959, p. 85). Near Que Que, Southern Rhodesia, he found a nest of a glossy starling, *Lamprolornis chalybeus*, containing a young great-spotted cuckoo several days old (the quills just appearing on the wings and tail), a young starling, fully feathered and estimated to be 10 to 14 days old, a dead young starling, estimated to have been dead for from 2 to 3 days, and trampled into the bottom of the nest, and one cracked, unhatched starling egg. Three days later the young cuckoo and the young starling were still in the nest; on the following day only the parasite was there and was seen being fed by the foster-parents; there was no trace of the missing young starling. Six days later the cuckoo, still in the nest, was fully feathered; the following day the nest was empty, but two days later the starlings were seen feeding the fledged parasite. Here we have another example showing the absence of eviction by the young cuckoo. In this particular instance it would appear that the starling must have hatched some days before the cuckoo.

In *C. levaillantii* we still lack such observations but there is no reason for thinking that the picture there is any different. Actually there are unpublished data of N. R. Hyslop (editorially referred to in Bokmakierie, vol. II, 1959, p. 19) that are said to confirm the absence of evicting behavior in this species. In the case of the pied crested cuckoo, *C. jacobinus*, alone, has anyone even suggested that eviction may take place and even here there is no conclusive evidence for it. In the few instances where this has been suggested it was not possible to establish that the ejection was deliberate or even that it was done by the nestling cuckoo.

Skead (1962, pp. 72-73) observed a nest of the forktailed drongo, *Dicrurus adsimilis*, containing a young jacobin cuckoo and three drongo eggs. Two days later one of the eggs was found on the

ground below the nest; the following day another egg was found there; still 4 days later the drongo chick, which had hatched in the meantime, was lying below the nest. The finding of these eggs and of the nestling drongo under the nest suggested (but only suggested) that the eviction was done by the young parasite. Skead was careful to point out that this inference required proof.

The estimated age of the young cuckoo was three days when the first of the host's eggs was found below the nest, and 8 days when the drongo chick was so recorded. If the eviction was done by the young cuckoo, this would imply a much longer duration of the evicting instinct than occurs in *Cuculus*, a genus in which the habit is well established.

It is impossible to state that the young cuckoo was not responsible, but there are other cases known where eviction definitely did not take place. Skead himself (1951, pp. 172-173) described a case in which a nestling jacobin cuckoo tolerated eggs and young in the same nest for up to 4 days, and another nest in which another young parasite made no attempt to evict the eggs for 4 days during which the nests were under observation. It not infrequently happens in a crowded nest that activity by one of the nestlings may sometimes result in the accidental pushing of one of the eggs or young out of the nest. Also, in parasitized nests, the young parasite often is larger and grows relatively faster than its nestmates and by successful competition with them for the food brought by the adults may starve them to death. In such cases the dead young are removed, not by the young parasite, but by their own parents as a matter of nest sanitation.

Furthermore, there are observations of still other nests in which the host young and the young jacobin cuckoo grew up together to the fledgling stage, and were seen together even after leaving the nest (Godfrey, 1939, p. 3; Bates, 1938, p. 125). These are clearly cases in which no eviction by the young parasite took place. In the two instances described by Skead, if any eviction by the young cuckoo might have been involved, it did not occur for some days after hatching, which is not the case in *Cuculus*. On present evidence it is doubtful that young *Clamators* have the habit of methodically and deliberately ousting their nestmates during the early stages of their nestling life.

An unusual type of host-parasite nestling relations was observed in India by MacDonald (1960, pp. 174-175). He watched a nest of a jungle babbler, *Turdoides striatus somervillei*, that contained a nestling jacobin cuckoo and a young babbler. The young parasite was

more advanced in its development than its nestmate and it was found to leave the nest and forage and then return to it to be fed by the foster-parents, who were more or less bound to the nest by the presence in it of their own less advanced chick. This was noted repeatedly, and suggested a degree of resourcefulness quite unexpected in a bird at the nestling-fledgling stage. It also was another instance of mutual survival, or, in other words, of the absence of evicting behavior by the young cuckoo.

FLEDGLING FEEDING BY ADULT CLAMATORS

The feeding of well-grown, fledged, young crested cuckoos by adults of their respective species has been reported for two of the four species of the genus. In no case has convincing, corroborative evidence been placed on record, but inasmuch as such behavior has an evolutionary interest as atavisms it is necessary to mention them here. The data are as follows:

In India, Gill (1925, p. 283) claimed that he had often watched adults of the jacobin cuckoo, *C. jacobinus* feeding fully fledged young of their own kind, and that koels, *Eudynamis scolopacea*, do this even more often and regularly. If this is correct the observations have not been reported subsequently by other field students, and it is possible that Gill mistook an adult female for a fully grown young merely because he saw it being fed by another jacobin cuckoo. It is known that this cuckoo does indulge in courtship feeding and it may be this was what Gill really saw. Thus, in South Africa, Godfrey (1939, p. 26) watched a melanistic and a pale morph of the jacobin cuckoo feeding on caterpillars on the ground. The pale bird was seen to pick up a caterpillar, pass it a few times back and forth along its beak, and then to approach the black-phase bird with this in its bill. It mounted the latter, gave it the caterpillar, and then mated with it.

Similarly, many years earlier, in northeastern Africa, von Heuglin (1869-1873) wrote of the great-spotted cuckoo, *C. glandarius*, that he thought it occasionally took care of young of its own kind. It is not possible to decide from his wording exactly what actions he witnessed, but it may have been more a matter of premigrational flocking, as no evidence of actual feeding of the young by the adults has been noted since anywhere in its range. That this may be the real condition from which von Heuglin gathered his impression is suggested by an observation of Ivy's (1901, p. 22), who, in eastern Cape Province, found a pair of adults with five young birds late in February. He considered that ". . . the old birds collected their broods previously

to migrating . . ." The most that may be said in the case of this cuckoo is that fledgling feeding is yet to be proved.

The mere act of courtship feeding, as shown in the jacobin cuckoo, is in itself an atavistic behavior, and if it should eventually be found to be coupled with even occasional feeding of fully fledged young (other than by mistaking them for adult females) this would further strengthen the suggestion that *Clamator* is a fairly primitive genus of parasitic cuckoos.

PLUMAGE VARIATIONS AND THEIR SIGNIFICANCE

Before we discuss the polymorphisms which have been well established in two of the four species of *Clamator*, *jacobinus* and *levaillantii*, it is necessary to review the extent and the nature of the variations found in the "normal" plumages as well as in their melanistic phases.

Although not pertinent to the immediate problem of polymorphism, the plumage variations of the climax species *C. glandarius* also may be described and discussed in this section of the paper, as they have pertinent evolutionary implications as well. *C. coromandus* calls for no comment here.

Clamator levaillantii

The "normal," i.e., the white-breasted, plumage has the entire underparts from chin to vent white, with black streaks on the chin, throat, breast, and upper abdomen, these streaks narrowing to shaft lines on the feathers of the sides, flanks, and undertail coverts, the streaks heaviest on the throat and upper breast; all the rectrices with broad white tips crossing both webs, and with a white patch on the outer eight primaries, this patch not visible from above in the closed wing because of the overlapping secondaries; underwing coverts white with very variable amounts of black markings. The entire upper surface of the head and body is solid black.

Here we find variations in the mental and pectoral stripes from specimens in which these dark marks are narrower than the white interspaces (the lateral portions of the feathers are here involved) to others in which the dark marks are broadened to the degree that they become practically coalesced to form almost solid black areas on the chin and upper throat. Although no geographic races of the stripe-breasted cuckoo are recognizable, much attention has been paid by authors to the degree of the variation, especially in the heaviness, the length and width, and the darkness of the blackish stripes on

the throat and breast of the adult birds. Gyldenstolpe (1921, pp. 246-247) considered some of this variability to be a matter of age, the stripes being narrower in younger birds than in older ones. He also thought the stripes were broadest and darkest in the males. Examination of large numbers of specimens, especially in London, convinced me that no correlation with age or sex may be maintained. Chapin (*in litt.*, 1961) wrote that while these stripes were variable throughout Africa, they seemed to average heaviest in specimens from the northeastern part of the continent—Ethiopia and Somalia. In five specimens from there in the American Museum of Natural History the throat was so broadly streaked as to be almost completely black. Examples of this extreme type came from Giamo, Bissidimo, Godja-Mariam, and Maraco, in Ethiopia, and from Warsangli-Mush Hated, 5,000 feet, in the Somali Republic. Another equally dark bird came from much farther to the south, from Machame, Tanganyika; in it the chin was fairly solid black, the throat less solidly so. In the British Museum I have seen specimens just as heavily marked with black from Mount Lotuke, in the Didinga Mountains of Sudan; also from Usambara Mountains, Pangani River, Tanganyika, and even one from as far to the southwest as Damaraland. All of these examples were adult males. Furthermore, in all the areas involved, other examples were much less heavily striped than those mentioned here.

One of the palest birds seen was from Tembura, in the Bahr-el-Ghazal Province of Sudan. It had only narrow black streaks on the chin and throat, these disappearing on the upper breast, in marked contrast to the Mount Lotuke dark extreme which not only had the black streaks almost coalesced on the chin and throat, but had these markings continuing very broadly over the entire breast, tapering caudally, but with narrow black shaft streaks on the entire abdomen, sides, flanks, and thighs. These abdominal shaft streaks were even more pronounced in the Usambara birds. Perhaps the extreme variant in this character of all the birds seen was a female from near Mombasa, collected together with five in the melanistic "*albonotatus*" plumage phase. In it the entire underparts were heavily streaked with black, from chin to vent. One from Kyambu, near Nairobi, Kenya, described by van Someren (1922, p. 51), was said to have the black stripes reaching the abdomen as well.

Turning now to the opposite extreme, a male from Gunnal, in Portuguese Guinea, from the other side of the continent, was almost as lightly marked as the Tembura bird. Recently, in a report on Gabon

specimens, Rand, Friedmann, and Traylor (1959, p. 271) noted the great variation in the underwing coverts and axillars; from almost wholly dull white to largely blackish. The Tembura specimen in London had no blackish at all under the wings. Years ago, a specimen from Danger River, Gabon, was used as the basis for the description of a very pallid "race" *caroli*. This specimen was studied in 1962 together with the Tembura one, as well as with a very extensive series of others. It was found to be paler, less streaked with black on the chin and throat, but the difference between it and the Tembura bird was not great enough to suggest that it might represent a distinct race. The type of *caroli* had the terminal white spots on the rectrices larger than in the Tembura specimen. The extreme pallor of *caroli* suggests, if anything, that just as in coastal Kenya *levaillantii* may produce completely melanistic phases (*albonotatus*), so elsewhere it may almost approach *jacobinus* in its lack of dark ventral markings. Certainly the geographic distribution of color extremes—darkest birds from Ethiopia, Somali Republic, Kenya, Sudan, Tanganyika, and Damaraland in South-West Africa, and lightest ones from Sudan, Gabon, Portuguese Guinea, and Rhodesia—indicate that they are haphazard in their occurrence, and hence not significant taxonomically. In none of these areas are the birds uniform in their variational trends.

Another variable character of the "normal" phase of *levaillantii* is the length of the feathers forming the crest. Here again, examination of long series from all parts of the range, tends to rule out the supposed significance of any local extremes. At one time in these investigations it seemed that birds from Ethiopia tended to have on the average longer crests than birds from elsewhere, but measurements failed to corroborate this.

The melanistic phase, originally described as a separate species under the name *C. albonotatus*, has been found (with one exception) only in the narrow coastal belt of Kenya, south to Usambara Hills, in Tanganyika, and north to southern Jubaland in the Somali Republic. I have been able to examine 21 of the 26 recorded specimens known to me. Since relatively few investigators have examined this plumage, and none with as ample material, the following notes on its variations are here recorded.

In general this phase may be described as being black all over, except for terminal white spots on the outer rectrices (this varies from the two outermost pairs to the four outermost pairs in different individuals), and a white patch on the inner webs of the eight outer

primaries. However, in four of the specimens there was some whitish, in the form of edges on the feathers of the throat, breast, abdomen, and undertail coverts. The amount of such whitish areas varied individually; in one unsexed example from Takaungu the feathers of the abdomen and the undertail coverts were broadly edged with grayish white; in another from the same place these pale edgings were very narrow. In this connection, it may be recalled that in our discussion of the variations in the normal phase, we described (*supra*) one example, collected together with melanistic birds, in which the entire underparts were white, heavily streaked with black from chin to vent. This specimen might equally well be described as a melanistic polymorph in which all the ventral feathers had white edgings.

The white spots at the tips of the outer tail feathers not only vary in the number of rectrices on which they occur, but also in the size of the individual spots; in some cases they are restricted to the outer web, in others they extend across both webs of these feathers. The presence of these tail spots is the only constant difference, aside from the total size of the bird, and its corresponding wing and tail dimensions, between this phase of *levaillantii* and the corresponding melanistic morph of *C. jacobinus serratus*. Very occasionally a specimen of *levaillantii* may lack these white tail spots, as in one taken near Lake Chahafi, Kibwezi, southwestern Uganda, reported by Pitman (1931). He implied that there was another similar one from former French West Africa in the British Museum, but I failed to find it when I examined the series there in 1962.

A number of the specimens of this black phase studied were in various stages of molt. They revealed that the juvenal plumage (or, at least, subadult plumage) is uniformly dull fuscous brown on the entire upper side of the body and head. In some examples the entire underparts, as well, were of this color, but in others the abdomen and sides were paler, more of a dirty brownish white. Even these young specimens had the white wing speculum as in the adults.

Clamator jacobinus

Unlike *C. levaillantii*, this species varies geographically in its plumage characters, and has been divided into three recognizable races. Typical *jacobinus*, a small race (wings 135.5 to 150; tail 146 to 172 mm.), with white throat and breast, the feathers of the lower throat and breast with the faint, dusky shaft streaks either practically wanting or pale and very narrow, hairlike lines, occurs in southern India and Ceylon, and is partly migratory as some of its members winter in

Africa. Another race, *pica*, similar in color characters, but larger in size (wings 149 to 164 mm.; tail 173 to 197 mm.), has two disconnected breeding ranges; one part breeds in Baluchistan, and in northern India from the Kashmir Himalayas west to West Pakistan, and Nepal, south to United Provinces, and Kutch, and winters largely in Africa, south of the Sahara; another large segment of the subspecies breeds in sub-Saharan Africa from Senegal east to Ethiopia and the Somali Republic, southward to Angola, northern portions of Northern Rhodesia, and southern Kenya. The third race *serratus*, similar in size to *pica*, is dimorphic in the southeastern portion of its range. Its pale morph is like *pica* but with the shaft streaks of the throat and breast feathers darker and often heavier, and the entire pectoral area and the sides of the body tinged lightly, or more heavily, with grayish. The dark morph is black except for the white wing patch. This is the race of Africa south of the Zambezi River, where it occurs only during the breeding season, October to March, wintering in tropical Africa along with *pica* and *jacobinus*. In the western part of its breeding range, especially in South-West Africa, it approaches in coloration the race *pica*; but the birds breeding there agree better on the average with pale *serratus*, and, furthermore, they lay white eggs like *serratus* (*pica* and *jacobinus* lay blue-green eggs). There is reason to believe that *serratus* may breed north to southern Kenya, but no form of the jacobin cuckoo has yet been found to breed in Tanganyika.

The chief evolutionary interest in the facts discussed in this section is that the range of variation in *C. levaillantii*, from the heavily striped pattern to the almost unstriped anterior underparts, as in the type example of "*caroli*" and in the Tembura example, comes very close to bridging the gap in this character between this species and *C. jacobinus* (fig. 14). We have also seen that the range of variation in the pale morph of the latter varies from birds with the chin, throat, and breast entirely white, devoid of any streaks or marks, to others with well-developed, but narrow, dusky shaft lines on the feathers of these parts. The lack of greater difference between the most definitely lined *jacobinus* and the least striped *levaillantii* almost establishes a variational continuum. There is a more sizable break between the dimensional characters of the two, but here again, the gap between the smallest *levaillantii* and the largest *jacobinus* is not very great in proportion to their size. Also, the juvenal plumages of the two species, and the melanistic phases are extremely similar, save in dimensions. The eggshell color of *C. jacobinus* in India and in northeastern Africa is similar to that of *levaillantii*. It is true that

in the more southern population of *jacobinus* (*serratus*) we find a markedly different egg type, but the difference here is just as great between sections of this species as between it and *levaillantii*. There can be no reasonable doubt as to the close relationship of the two species.

Inasmuch as it is thought that the southern *serratus* is nearer to ancestral *C. jacobinus* than are the other races of the species, it would follow that the evolutionary trends in plumage pattern involved a

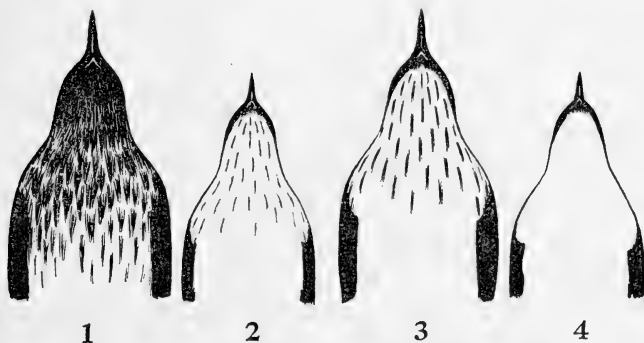


FIG. 14.—Variation in pectoral markings.

Clamator levaillantii: 1, Darkest; 3, palest.

Clamator jacobinus: 2, Darkest; 4, palest.

loss of the pectoral shaft stripes giving rise to *C. j. pica* and *C. j. jacobinus* on the one hand, and a great intensification of the same character giving rise to *C. levaillantii*. From the *serratus*-like primordial stock both developments arose and diverged.

It may be remarked that it seems (to human eyes) that some plumage characters of no great biological significance are tenaciously retained during evolutionary changes while others of no more obvious utility are altered. An example of the former is the white wing patch found in both the pale and the melanistic morphs of both *jacobinus* and *levaillantii*, although this may have a recognition and a releasing function in both species.

Clamator glandarius

The one feature of greatest evolutionary significance, or, to put it in a different way, the one phylogenetic clue of greatest interest in the plumages of this, the climax species of the genus, is the fact that

its juvenal plumage has the remiges extensively reddish, suggesting a relationship with *C. coromandus*. Aside from this, there is only one point worth mentioning in any detail, the possible geographic variation in the adult *C. glandarius*.

Clancey (1951, p. 141) separated the population breeding in Africa south of the Sahara from the nominate, Mediterranean basin birds, and gave them the name *choragium*. The characters of this southern race were smaller size and warmer buff on the throat and breast with less pronounced dark shaft streaks on the feathers. Judging by Clancey's account, Gilliard examined for him the material, totaling 101 specimens, in the American Museum of Natural History and apparently agreed in considering the two populations as distinguishable. In the course of my studies I have examined nearly 200 additional examples, including 177 in the British Museum, and I found that there was very extensive overlapping in all these characters. The buff tone of the throat and breast in fully adult birds may average very slightly warmer in *choragium*, but great care must be taken to compare birds of the same age, as the young of both populations are warm tawny buff on the throat and breast and adults of both largely lack this color and are not more than pale buffy cream with a slight ashy tinge. I could not find any constant difference in the development of dusky shafts on the feathers of this area in the two groups of birds. Furthermore, the size characters showed more overlapping than the figures given in Clancey's paper, and at best were not more than a slight average difference, hardly enough to warrant nomenclatorial recognition.

Using only breeding season examples, to eliminate possible migrants of the other population, I found that in males the wing length varied from 190 to 223 in Mediterranean birds, from 185 to 218 in southern ones: The tail length in these males varied from 186 to 226 in Mediterranean examples, from 181 to 219 mm. in southern ones. The females showed similar overlapping. Finally, as a test, I found myself unable to relegate the majority of specimens to subspecies without looking at the localities on their labels. I therefore do not accept *choragium* as a valid race, at least not as a race of utility in taxonomic work.

It may be mentioned that I examined these birds with the expectation that *choragium* would be corroborated, as I was aware of interesting differences in the host relations and host-parasite adaptations in the two populations. I can only look upon the results as providing unexpected support for the relative recency of this cuckoo as a breeding bird in sub-Saharan Africa, a conclusion already suggested by a

study of their relatively poorly adjusted host relations in the African part of their range.

The situation present in the sub-Saharan *Clamator glandarius* as compared with that in the circum-Mediterranean segment of the species is reminiscent of Thorpe's (1930) biological races in insects. He called attention (p. 189) to instances among species of insects and allied groups in which geographically isolated populations with little or no structural or pigmentary differences were definitely differentiated biologically or behaviorally. These he considered essentially the same as subspecies, but in which the racial characters are aspects of the living rather than of the preservable parts of the specimens. As I have already indicated I do not think it advisable to give separate taxonomic or nomenclatorial rank to the two sections of *Clamator glandarius*, as the size and color characters ascribed to *choragium* are too slight and the overlap too great to make it a "usable" subspecies, although *choragium* does reveal a trend toward differentiation, as yet not well developed, and there is in its life history a biological difference in its host relations and in its range of host selections. The very fact that its behavioral character results in relatively poor coordination in its host relations, coupled with the independent fact that its structural modifications are still only faintly developed, suggests that "*choragium*" is a new, possibly as yet only an incipient, race.

One further item in the plumage cycle of *C. glandarius* deserves mention. Its juvenal plumage is blackish on the top of the head and nape, not gray as in the adult. Because of this, Jourdain (1925, p. 661) suggested that this might have been produced through adaptive evolution to achieve some degree of resemblance to the plumage of the nestlings of its Palaearctic corvine hosts. Jourdain stressed that the only conspicuous parts of the young bird while in the nest are the crown and nape, and he accordingly discounted the pale tawny chin and throat coloration. However, it may be recalled that the critical moments for the nestling are when the foster-parent comes with food. At such times the young cuckoo, as well as host young, raise their heads and open their mouths widely and clamor for food, and at such moments the throat would be no less visible than the crown and nape. I cannot help but consider Jourdain's suggestion as an "armchair speculation," and it certainly does not apply to the sturnid hosts the parasite uses in Africa. On the other hand, Cott (1940, p. 422) was convinced enough to write that the nestling of this cuckoo has a plumage ". . . whose crown has been influenced by natural selection, but whose throat has been neglected—so that while

the latter resembles that of its parents, the former imitates that of its nest-mates . . .”

POLYMORPHISM

Two of the four species of *Clamator* have produced well-established melanic morphs or plumage phases in restricted portions of their respective ranges. These two are *C. jacobinus* and *C. levaillantii*, and it so happens that the black phases of the two are extremely similar. Their geographic ranges are quite dissimilar in extent, however; that of *jacobinus* occupies a large area of southeastern Africa, while the corresponding one of *levaillantii* is restricted to a narrow coastal strip of northeastern Tanganyika and of Kenya.

Both of these morphs appear to be, in every way, good examples of polymorphism in the sense defined by Ford (1945, p. 73). In his definition a polymorphic species is one in which there are two or more distinct phases or forms simultaneously in the same habitat, even in the same deme and the same local population, and in which these forms occur in sufficient numbers that even the least common of them is too numerous to be accounted for by a continuous series of recurrent, identical mutations. To this basic concept may be added, as was pointed out by Carter (1954, p. 259) the further thought that the characters of these polymorphs must be such that they do not blend on crossing; in other words, they must be controlled by single genes, or at least by small groups of genes that are closely linked in their mode of inheritance. Otherwise, the normal interbreeding that goes on in any local population of a species would tend to transform these polymorphs into a broad but continuous spectrum of variation. In the case of *C. jacobinus* we have ample field evidence that crossing between the two color morphs takes place frequently and yet no intermediate plumages are known. For *C. levaillantii* we still lack field observations of similar crossing between the morphs as little work has been done in the restricted area of its polymorphism.¹ In

¹ As described in our discussion of migratory behavior (p. 86) Lamm noted seeing two *levaillantii*, one in the normal and one in the black phase, at Vila Luisa, southern Mozambique. There can be no reasonable doubt as to his identification of the pale morph, and if the two were really a “pair” this would be a case suggesting that the situation between morphs in this species is the same as in *jacobinus*. The fact that the locality is so far south of the known range of the melanistic morph of *levaillantii* makes this sight record somewhat uncertain. Furthermore, Lamm’s notes are not conclusive as to whether the two birds were really a pair. He merely saw a black-plumaged bird near the normal *levaillantii*; he observed no sign of mutual interest between them, although he wrote, “probably a pair.”

this connection it may be recalled that Stresemann (1947, pp. 518-519) suggested that the ". . . allele-producing mechanism has besides some physiological effect increasing viability in this special environment (but not elsewhere) which results in its being favoured by selection . . ." In support of this suggestion he pointed out that a shrike, *Laniarius ferrugineus sublacteus*, also has a melanistic morph (*L. nigerrimus*) in the same limited area of coastal Kenya and the lower portion of the valley of the Tana River.

While the restricted geographic coincidence of melanistic polymorphism in two widely dissimilar and unrelated birds as a cuckoo and a shrike may be suggestive, it remains that in neither species do we have as yet any observational data as to the relative abundance of the two plumages, to say nothing of the frequency of crossing between their phases. In the absence of such information we can only interpret the situation in *C. levaillantii* as probably similar to what we know in the related *C. jacobinus* in southeastern Africa, and in that species it is difficult to see that either morph has any selective advantage over the other. In connection with Stresemann's suggestion, it may be recalled that *C. jacobinus* also occurs in coastal Kenya and the Tana Valley, and has produced no melanistic morphs there although it has done so far to the south. If there were something in the ecological situation of coastal Kenya that might favor such melanisms we might expect it to have produced some visible manifestation in *C. jacobinus* as well. That local ecology is not directly important in the establishment of polymorphism is further indicated by the fact that in the extensive area of southeastern Africa where *jacobinus* has two phases, *levaillantii* occurs in a single, "normal" or "pale" phase. In other words the two species are sympatric in the two areas where one and not the other is polymorphic.

The melanistic morph of *C. jacobinus* occurs as a breeding form throughout Natal, the eastern Cape Province, the eastern half, or more, of the Transvaal, the Orange Free State, and to Bechuanaland (Mahalapye), Southern Rhodesia (Bulawayo), Northern Rhodesia (Livingstone), and Nyasaland (Misanje). It is decidedly rare in the Rhodesias and Nyasaland, and finds its greatest abundance in Natal, the eastern Cape Province, and eastern Transvaal. It also occurs in southern Mozambique, but I know of but one actual specimen record from there, and it had no exact locality other than "Mozambique" on its label.

The corresponding black phase of *C. levaillantii* is known, as far as I have been able to learn, from some 26 specimens in the museums of the world. Of these, no fewer than 18 were collected within 50

miles of Mombasa (Mombasa, Kilifi, Mazeras, Takaungu, Rabai Forest, Sokoke Forest); 1 came from Malindi; 3 from the lower portion of the Tana Valley (Kosi, Kau, and near Lamu); one example was recorded from southern Jubaland (Jebeir), the most northern locality from which the black morph has been reported; the type specimen (of "*albonotatus*," under which name this morph of *levaillantii* was first described as a new form) was collected in the Usambara Hills, northeastern Tanganyika, and another was taken not too far away, on the Pagani River. The one remaining specimen, now in the collection of the Academy of Natural Sciences, Philadelphia, was taken at an altitude of 10,000 feet on Mt. Kenya, in February 1919! This locality is far removed geographically and ecologically from all the others. The specimen was originally in the Blayney Percival Collection, and since Percival is generally considered to have been a careful and reliable labeler of his birds, there is no valid reason for questioning this record.

It does, however, point out an interesting fact, namely that the tendency to produce melanistic morphs is not absolutely restricted to the area where these have become well established. While it cannot be proved that this specimen from the high slopes of Mt. Kenya was not a migrant from the coastal lowlands, this is extremely improbable. It would be a strange migration indeed for a bird of the hot coastal belt to migrate to an altitude of 10,000 feet on Mt. Kenya. Furthermore, we have no other evidence of the melanic morphs spreading out from their restricted habitat, such as we might expect if they were regularly migratory. Yet, it must be admitted that Percival (in Bannerman, 1910, p. 704) wrote that "*albonotatus*" seemed to visit the coastal belt of Kenya for about 6 weeks only in the year, which suggests seasonal movement. On the other hand, he collected two examples there in March, only a few weeks different in season from his Mt. Kenya bird. It seems, from all these considerations, more likely that the latter was a case of an individual melanism cropping up as an isolated occurrence. It may be mentioned that there is evidence of similar, sporadic, widely spaced cases of melanic polymorphism in *C. jacobinus* as well.

In the latter species occasional black-phase birds, indistinguishable from southeast African melanistic *serratus*, have been taken at Port Gentil, Gabon (November 3), south of Lake Tchad (in July), at Kulme, Darfur, Sudan (July 11), Kordofan, Sudan (no date) and at Sagon River, Ethiopia (June 4). Reichenow (1902, p. 78) listed the Kordofan record in the synonymy of the pale-vented *jacobinus*, not

of *serratus*. However, Strickland (1850, p. 219) was aware of the difference, and commented that to his knowledge this “. . . Cape bird has never before, I believe, been obtained to the north of the equator . . .” Certainly the November bird from Gabon, in very fresh plumage, cannot have been a migrant from southeastern Africa, where at that time of the year *serratus* is breeding. Furthermore, the Kulme and Lake Tchad birds, taken in July, and the June specimen from Sagon River, are all in the same stage of molt as Natal birds are in February. This indicates that whether they were resident in the areas of capture, or whether they wandered there from elsewhere, they may not have come from southeastern Africa, where the molting season differs by a third to a fourth of a year from theirs.

The ranges of the melanistic phases of *C. jacobinus* and *C. levaillantii* are not readily expressed in terms of vegetational areas. Thus, if we take Keay's 1959 Oxford "Vegetation Map of Africa south of the Tropic of Cancer," we find that the black-plumaged *C. j. serratus* overlaps in its breeding range, the "Relatively Dry Woodlands and Savannas" (characterized by savannas of tall grass with *Acacias* as well as other trees) and the "Temperate and Subtropical Grassland" (pure grassland above 3,500 feet). The melanistic phase of *C. levaillantii* appears to be contained within, but is not coextensive with, the "Coastal Forest Mosaic" area.

To clarify the recorded data, it may be stated at this point that the old report of a black-phase *serratus* from Denkera, Fantee, Ghana, listed by a number of authors in their compilations, is based on an error. The actual specimen involved, examined by me in London in 1962, is not a *Clamator* at all, but a black cuckoo, *Cuculus cafer*. Similarly, the supposed record of melanistic *serratus* from Lamu, Kenya, cited by several writers on east African birds, is actually based on an example of the black phase of *C. levaillantii*, to which it is properly referred in the present study.

To return to Ford's illuminating appraisal of the whole question of polymorphism, it appears that the situation in the two species of *Clamator* fits the definition of what he terms neutral polymorphism. It may be explained that Ford distinguishes three types—transient, neutral, and balanced polymorphism. The first is, as its name suggests, a polymorphism in the process of spreading through a population, but once it becomes fixed and ceases to spread it is no longer to be termed transient, but becomes either neutral or balanced. When a variant phase, or morph, has a selective advantage only as long as it does not dominate numerically the total population in which it

occurs, and loses this advantage when it becomes more widely prevalent, it is said to be a balanced polymorphism. However, when such a form appears to be without obvious selective value or adaptive advantage, it is termed a neutral polymorphism. It is not clear that the distinction between neutral and balanced polymorphism is biologically factual; it might be better to say that the neutrality of certain balanced polymorphisms is merely an observational inference rather than an established genetic fact. It is in this restricted sense that the situation in *Clamator* may be described as neutral. In the light of present evidence, at least as far as *Clamator jacobinus* is concerned, the "normal" morph and the black phase seem equally well adapted to their common environment. The birds interbreed freely and act as though they recognize no differences between them, and furthermore the black form is not noticeably spreading geographically or becoming increasingly numerous where it occurs together with the white-breasted form (and it is not known to occur anywhere as the sole morph). In some localities it is apparently as common as, and in a few spots even more numerous than, the pale morph, but there is no evidence to suggest that the ratio has changed appreciably in the past half century or more of observations. It must be admitted that this absence of evidence is not nearly as good a support as would presence of negative evidence have been. The "evidence," if it may so be termed, is chiefly the memory and recollections of observers of long residence, unsupported by critical records and notes.

In the case of *C. levaillantii* we can only assume that the situation is also one of neutral polymorphism, as we do not have the direct evidence available in *C. jacobinus*. It seems, however, a safe assumption.

Polymorphism is an expression of gene frequency, and neutral polymorphism implies a fairly stable frequency picture. Inasmuch as the occurrence of melanistic morphs of both *levaillantii* and of *jacobinus* away from their geographically restricted areas of developed neutral polymorphism is so sporadic and infrequent, it follows that these two wide-ranging species, each with geographically continuous, uninterrupted, nonfragmented distribution patterns, have local populations whose gene pools seem to be fixed and seem to be kept unavailable to adjacent populations of their own kind.² There

² In the case of *C. jacobinus* this statement is intended to cover only the African part of its range; its extensive Asian population is of course effectively cut off from the larger African one. No black-phase birds of this cuckoo have ever been noted in Asia (from which area I have examined at least 200 examples, as well as read and checked the many observations and records in the literature).

may possibly be some unknown and, as yet unsuspected ecological factor in the area of polymorphism of each of these species that has made possible a local decrease in selective pressure and thereby enabled two morphs of each to develop in a state of passive neutrality. This may be something akin to what Stresemann vaguely suggested, although transposing the factor from the "allele producing mechanism" to the environment. There is no evidence even tangential to this concept that may be cited, and the thought is merely inserted for its suggestive value. Considering that both species are highly migratory, at least in their southern sections (exactly the section where *jacobinus* is polymorphic), it is difficult to account for this apparent genetic isolation in the light of present knowledge. It seems that in coastal Kenya, Percival's statement (*cit. supra*) notwithstanding, *levaillantii*, with its local black phase, is relatively nonmigratory, but no such assumption can be maintained for either in southeastern Africa. The absence of migrant, or of "wintering" examples of black-phase *C. jacobinus serratus* from equatorial Africa during the southern winter, when it is known that both phases are absent from their relatively well-observed austral breeding range and have presumably gone north, is a real puzzle. This is discussed more fully in our account of migratory behavior (see pp. 84-85). In the present connection it may be hypothesized that, wherever they may "winter," all the individuals of southeastern *serratus* return to their home area for breeding, and thus remain unmixed with their adjacent conspecific populations.

Aside from the well-developed melanistic morph in the adults of *jacobinus* and *levaillantii*, the latter species also has a rufescent juvenal morph, reminiscent of the hepatic phase of the young in *Cuculus canorus*. I know of only two examples of this rufescent phase, both from the northeastern portion of the Republic of the Congo (former Belgian Congo). One such bird, a young male, taken at Poko, in the Uelle district on July 31, now in the British Museum, is bright cinnamon rufous above and below, only the remiges and retrices being darker, less reddish, as in the "normal" juvenal. The other one came from near Beni, in the Ituri district. Another, possibly partial, rufescent bird may be one mentioned by Granvik (1934, p. 24) as having the undertail coverts pale rufous, although the rest of the plumage was probably "normal" as it evoked no comment from the describer.

MIGRATORY BEHAVIOR

The evolutionary picture of migratory behavior in the genus presents some peculiar features. All four of the included species are

strictly migratory in some parts of their respective ranges and not in other parts. (In the case of *C. coromandus*, the available evidence is not conclusive about an area of permanent residence, and, hence, of a population of nonmigratory birds.) The extent of migratory movement varies from none at all to thousands of miles. All three of the species breeding in South Africa (*glandarius*, *jacobinus*, and *levaillantii*) are absent from that area during the southern winter; all three have resident populations in tropical Africa. The first named of these is present in its Mediterranean breeding grounds in the Iberian Peninsula and northwestern Africa only during the northern summer, and then migrates to equatorial parts of Africa, apparently chiefly in the eastern half of the continent. The migration of this section of the species is thus exactly the opposite, both in direction and in time of the year, from that of the South African *glandarius*. In other words, we find in these cuckoos that geographic segments, not necessarily even subspecifically distinct, differ markedly from other conspecific segments in their migratory behavior. It need hardly be added that in the majority of birds that have spatially distinct breeding and nonbreeding quarters, migration is an important, well-formulated and patterned, presumably evolved and inherited, part of their annual life cycle. Yet in the crested cuckoos of the genus *Clamator*, this migratory behavior is manifested only in sections of each of the included species.

In this geographic fragmentation of migratory behavior within the members of each species, we have something that may be likened to partial migration, with the difference that here the "partial" element is geographic, not individual. Partial migration is a term used chiefly for species in which some individuals are regularly migratory while others, breeding in the same area, are nonmigratory, resident birds. Inasmuch as there is no evidence to prove that the migratory South African populations are ecologically or geographically cut off from their nearest resident counterparts in tropical Africa, we cannot postulate an interference effectively isolating them into discrete, non-intercommunicating colonies or gene pools. Even allowing for a reduced frequency of such intercommunication, we may come back to something akin to partial migration (in an overall species view) as a valid way to express their migratory tendencies.

Partial migration of the more usual sort has been studied in the North American song sparrow by Nice (1937), and in a variety of European passerine species by Lack (1943-44). Their findings are of interest here. Nice (1937) found that in the song sparrow,

Melospiza melodia, in the Columbus, Ohio, area, migratory and non-migratory behavior was not correlated with age, and apparently was not a matter of inheritance. Thus, nine resident fathers had seven resident and two migratory sons, and nine migratory fathers had seven resident and four migratory sons. Among 61 males, it was found that 24 remained consistently resident, 31 were consistently migratory, and 6 changed from one to the other of these behavior groups. Among 43 females, 5 were consistently resident, 37 always migrated, and 1 changed from resident to migrant. Some years later Lack (1943-44) reported on a study of partial migration in a number of species of European birds, and showed that in all cases the females and the young of the year showed a noticeably greater tendency to migrate south in the autumn than did the adult males.

Baker (1942, p. 4) was aware of the partial nature of the migration of cuckoos other than *Clamator*. He went so far as to conclude that "... most genera and, indeed, most species of migratory Cuckoos include a race which is more or less sedentary. For instance, the Common Cuckoo, the most migratory form of Cuckoo, has a race, the Khasia Hills Cuckoo, which can hardly be called migratory at all. It breeds in the eastern sub-Himalayas and spreads into the plains of Burma and India in winter, while some individuals remain all the year round in their summer quarters. If ... migration has in many cases been forced upon birds because of the insufficiency of food supply during the breeding season it may well be, ... that cuckoos were originally tropical or sub-tropical oriental birds and their extreme limits, East and West, are those to which they have extended under this pressure ..."

In his recent (1962) survey of bird migration, Dorst noted that a considerable number of species of birds are composed of sedentary, migratory, and partially migratory populations, which could be looked upon as "physiological races" or sections of the total population of each species. From this he drew the logical conclusion that migration cannot be regarded as a specific character as it really belongs within the framework of populations within the species.

In some species of other birds migration is a characteristic of one race or subspecies and not of another. A case that may be mentioned is the Oregon junco, a North American finch studied experimentally by Wolfson (1942). This bird has a migratory and a purely resident race in northern California. To test their migratory tendencies Wolfson experimentally subjected groups of individuals of each kind to increasing numbers of hours of light, either natural or artificial,

but only the individuals of the regularly migratory race responded by becoming restless. This indicated that not only was a predisposition for migratory behavior necessary but that it could be manipulated. What can be manipulated experimentally by the investigator may also be effected out of laboratory conditions by "natural" causes.

At this point it seems useful to note the results of some recent studies because they correct a concept of migration based too largely on what has been recorded in north-temperate areas of the world. The pattern of migration there, with its easily accepted geographic inferences and correlations, is usually expressed in terms of Pleistocene climatic fluctuations. However, Moreau (1951) has shown that bird migration is probably as old as bird flight and that what happened during the Pleistocene in Europe and North America merely determined the geographic details of the migrations of individual species; but not the migratory behavior itself. It is true that most of the major, "best organized" migrations of considerable geographic magnitude seem to have reflections of Pleistocene events, but we realize that migration may have begun anywhere, anytime, with different groups of birds (Drost, 1950, p. 231). Pleistocene glaciation was not its cause. Moreau (1951) and Mayr and Meise (1930) indicated that migration may have originated in any localities where seasonal food scarcity may have caused some birds to move away seasonally and thus have a better chance of survival. Ostensibly, it would seem that this would be acted upon by natural selection, and in this way migratory behavior would become established, with or without any influence of Pleistocene glaciation, and, in some cases, probably was much earlier than Pleistocene in origin. In defense of this argument Moreau (1951, p. 247) cited cases of migration entirely within warm areas, and mentioned among them ". . . the Indian population of the cuckoo, *Clamator jacobinus*, which travels all the way to East Africa after breeding . . ."

Cuckoos, as a group, are birds with a great tendency or predisposition toward migration. Many years ago, W. L. Sclater (1906) calculated that of the 814 species of birds then known to occur in South Africa, 731 were resident, and only 21 were to be considered as African migrants (as distinguished from European and Asiatic winter visitors), and of these 21 no fewer than 9 were cuckoos. Many years prior to Sclater, Emin Pasha, prior to 1888, (published by Schweinfurth, et al., 1888, p. 392) noted the seasonal wanderings of a number of purely African savannah birds in "Equatoria" (the southern part of the present Sudan and the adjacent area of the Republic of the Congo), among which he mentioned *Clamator*.

It is among the cuckoos, purely insectivorous in their feeding, that we find some of the most remarkable of geographic migrants. We may take, as an example, the long-tailed cuckoo, *Urodynamis taitensis*, that makes an unusually long, and largely nonstop, overseas journey from its New Zealand breeding grounds to the islands of Polynesia, some of which are as much as 4,000 miles away. (Bogert, 1937). Another notable example is the little bronze cuckoo, *Chrysococcyx lucidus*, also a New Zealand bird, that goes more than 2,000 miles across the South Pacific to the Solomon Islands (Fell, 1947). The common cuckoo of Europe makes a similarly impressive journey from its northern breeding area to tropical and even to southern Africa. In fact, numerous writers have made particular mention of the fact that the young of the year of this species make this spectacular trip by themselves with no possible aid from, or accompaniment by, the adults of their own kind, with whom they have had no experience.

The concepts of migratory tendencies, even if they are not more than a periodic psychobiological restlessness, originally not rigidly correlated with, or controlled by, heredity, and of migration apart from the rigid seasonal climatic fluctuations of Pleistocene glaciation-induced patterns, make it possible to look upon the *Clamator* situation as less enigmatic and less paradoxical than it first seemed to be. Considering the pronounced migratory tendencies of its relatives in the subfamily Cuculinae, it would be surprising if the species of *Clamator* were not also somewhat migratory. The extent to which this behavior is developed differs in the four species of the genus. To explore these differences further, we may now turn to the situation in each species, as far as the present, still incomplete, data will permit coordinated presentation.

Clamator jacobinus

It is definitely known that the population (subspecies *serratus*) that breeds in Natal, Transvaal, Cape Province, and Southern Rhodesia, is absent from those areas from late March to October (southern "winter"), and that individuals of the pale morph of this race have been collected during these months in Nyasaland, in the open grasslands of the southern and eastern parts of the Republic of the Congo, former Belgian Congo, (Aru in the Upper Uele, Mahagi Port in the Ituri, and near the base of Ruwenzori) and in Uganda (Mohokya, Fajao, and Kebusi in May, Butiaba in November). In Darfur, Lynes (1925, p. 354) found *serratus* (recorded by him as *jacobinus*, but corrected by Jackson and Sclater, 1938, p. 497) in June and August.

In Sudan the pied crested cuckoo generally is reported by Cave and MacDonald (1955, p. 174) to be a fairly common nonbreeding visitor from March to October in the southern part of the country, from June to late August in Darfur. It may be noted, however, that many years ago Emin collected an egg of this cuckoo at Lado (Hartlaub, 1881, p. 114) while Butler (*in* Sclater and Mackworth-Praed, 1919 p. 642) stated that it breeds near Khartoum, where he found newly fledged young on October 5 (Butler, 1908, p. 245).

In British Somaliland (now part of the Somali Republic) Archer and Godman (1961, pp. 663-668) reported it as present in May and June, the main breeding season of many potential passerine hosts. There are as yet no definite breeding records from that area but the pied cuckoo may well prove to breed there.

In Ethiopia, *serratus* has been collected as early as April 7 to 8, at Gato River, near Gardula (Friedmann, 1930, pp. 268-272) together with examples of the race *pica*, and at Sagon River, June 4. In Eritrea, K. D. Smith (1957, p. 309) classed it as a migrant, present from June to September, possibly breeding there in summer.

In Angola this cuckoo (subspecies *pica*) is found only from October to May, from Huila and eastern Moçâmedes to Cuanza Norte to Luanda and along the coast from Benguela to Cuanza; it migrates north of the equatorial forest in "winter." For these summary data I am indebted to M. A. Traylor of the Chicago Natural History Museum, who further informs me that there are breeding records from Chibia in February and from Huila in December, and that some of the Huila specimens show an approach to the pied phase of *serratus*.

In Tanganyika, Moreau (1937b, pp. 22-23) noted that while no race of *C. jacobinus* had yet been found to breed in that country, pied morphs of *serratus* were known to appear there as migrants, as well as the paler, white-breasted *pica*, some of the latter race presumably coming from India. He further noted that examples of this cuckoo from extreme western portions of Tanganyika may belong to a ". . . population different from that occurring in the rest of the territory; the date of the influx accords with a possibility that they might be birds coming south from spending their off-season in Darfur and the Sudan." Thus, at Kigoma, in late October, Pakenham found *pica* became abundant, and he found that a female collected as a specimen record had an enlarged ovary, ostensibly a bird on its way to its breeding grounds.

In another paper, Moreau (1937a, pp. 5-7) reported that white-breasted birds (*C. j. pica*) had been collected in northern, central and

southern Tanganyika between December and April. All his own northern Tanganyika records were of “. . . silent non-breeding birds in worn plumage or very slow and irregular moult like the February birds of extreme southern Tanganyika . . . This influx of non-breeding birds into northern Tanganyika fits in strikingly with Whistler's hypothesis that the Indian population migrates to Africa after breeding in the northern summer; and clearly the birds, also non-breeding, that are so common in Darfur June to September must have quite a different origin . . .”

In Kenya and Uganda, Jackson (in Jackson and Sclater, 1938, pp. 495-496) found *pica* to be a local migrant, rarely if ever remaining long in one locality, arriving in November and leaving in April and May. He noted these birds, apparently traveling north, from March 20 to April 16 at Nimule, Uganda, and moving south in November at Lake Albert. In the Nyando Valley he found them common early in May and scarce at the end of that month. “The same influx and departure after a few weeks' sojourn takes place in the coast and bush-veld regions of Kenya Colony . . . It is particularly plentiful in the Taru wilderness in November and December, and again in April . . .” However, there is now definite evidence that *pica* breeds in Kenya (Ngong) and in Uganda, so here it appears that there are resident birds, migrants from elsewhere in Africa, and migrants from India, making the resulting situation difficult to interpret with certainty in many specific instances. The intra-African migrants appear to be of both *pica* and *serratus* stocks. Similarly, there is some evidence that both *pica* and *jacobinus* wander to Africa from India.

It is unfortunately true that, so far, we have no direct proof, of marked individual birds, demonstrating the migration of pied cuckoos from India to Africa, but there are inferential considerations that strongly point in this direction. Long ago Whistler (1928) compiled an account of the postulated migration in the hope that it might stimulate observers in India to fill in the gaps in the information he was able to bring together. He showed that the bird (*pica*) is extremely numerous in northern India during the rainy season, when it breeds there, and that it is definitely absent from there the rest of the year. He expressed his attitude by stating that if the birds do not leave India and go to Africa “. . . we cannot say at present where so great a mass of individuals can winter unrecorded; it can only be in southern or southeastern India or in Ceylon . . . Legge's evidence appears to have ruled out Ceylon. As to southern and southeastern India, we have no definite evidence either for or against the supposition . . .”

In a later paper (1931, p. 193) he pointed out that the absence of examples of north Indian birds (*pica*) in the extensive series collected in southern India (*jacobinus*) at all times of the year ". . . virtually settles that our northern migrants go to Africa . . ."—a conclusion which has been accepted and implemented, without definite proof, by many others since Whistler's paper. Smythies (1953, p. 326) found that the jacobin cuckoo ". . . seems to leave Burma altogether in the winter, possibly migrating to Africa." In his recent compendium on Indian ornithology, Ripley (1961, p. 175) stated that *pica* (*serratus* of his book) reaches, on its winter migration, Gujarat, Bombay, Andhra, and northwestern Madras. ". . . The main wintering range appears to be to the west, south of the Sahara in Africa. Rainy season wanderings of this form and the next (*jacobinus*) prevent exact definition of the breeding zones in central India." Meinertzhagen (1954, p. 308) reported that in Arabia, a presumably logical area through which migrants between India and Africa might be expected to pass, the species was known as a migrant in the southwestern part of that peninsula, where specimens were obtained near Aden on March 31 and April 22, in the Amiri district in May, at Hadda near Mecca on April 2. He noted that a pair was obtained in Asir on June 26, which "may denote breeding." If these were breeding birds, and not delayed migrants, they constitute the only evidence for the pied crested cuckoo in Arabia other than on migration. On the basis of extensive personal experience with both Asiatic and African birds, Meinertzhagen concluded that some of the birds that breed in northern India and Baluchistan appear to go to Africa in the northern winter.

Grant and Mackworth-Praed (1948, pp. 171-172) attempted to study the migration of these birds on the basis of the dates of molting specimens in the British Museum. They started with the opinion that Indian specimens should be in molt from September to November, South African breeders, from April to June, and birds from other parts of Africa, from June to August. The fact that in India birds taken from September to November were in molt was in line with these dates, and from all these considerations it was thought that any molting examples taken in Africa during September, October, and November should be Indian migrants. Their examination failed to find any such material and they were forced to conclude that none of the African records could be considered definitely as migrants from India, and they ended with the statement that the ". . . only evidence we still have of this species visiting Africa from India in the non-

breeding season is the fact that it does leave India . . ." In 1962 I went over the material in the British Museum with a hope of finding some clues that Grant and Mackworth-Praed might have overlooked, and to examine recently acquired specimens that they had not seen. My results suggested a greater spread of months for molting of African birds, which clouded or obscured the whole picture to the degree that it was not feasible to demonstrate Asiatic origins by molting dates.

Clancey (1960, pp. 27-31) has, I think, made the only convincing contribution to this problem. He stated that not only do north Indian birds (*pica*) migrate to Africa, but he found that so do many of the smaller, typical *jacobinus* of southern, peninsular India and Ceylon. The birds of this subspecies are identifiable by their smaller size and consistently white throats and breasts (like *pica* in this latter character), and they are known to breed only in India, Assam, Burma, and Ceylon, but they occur in Africa as far south as Nyasaland, Southern Rhodesia, and southern Mozambique. The African records fall between September and April, which agrees with the fact that the birds should be back in India for the breeding season. Unlike north Indian *pica*, the race *jacobinus* is only partially migratory, some individuals remaining throughout the year in southern India and Ceylon while others reach Africa where they disperse over a wide area. The fact that some south Indian birds do migrate to Africa increases the probability that similar movements occur in north Indian *pica* as well.

The migration of *C. jacobinus* between India and Africa, does have some peculiar features. Ali (*in litt.*) has informed me that as far as he knows no other long-distance land migrant arrives in India at the commencement of the southwest monsoon season as this cuckoo apparently does. He further assured me that there is no evidence that any seasonal lack of insect food could operate as the reason for this bird to leave India after the close of the breeding season.

As discussed elsewhere in this report (p. 51) it seems that the southern African population (*serratus*) of *C. jacobinus* is the oldest, most primitive segment of the species, and of the genus, as it exists today, and that after it gave rise to *pica* in equatorial Africa, the latter spread to Asia and became established there. The present migration of *pica* between northern India and Africa thus is an annual reflection of an original movement in the past history of the species, a situation existing (or, at least, so interpreted) in many other migratory birds. Ticehurst (1922, p. 531) postulated a route

from northern India to Africa for a number of Indian breeding species that are absent from there in winter; among them are *Agrobates g. familiaris*, *Caprimulgus e. unywini*, *Merops apiaster*, *Glareola pratincola*, *Cuculus canorus*, and others. To these may be added another cuculine species, the lesser cuckoo, *Cuculus poliocephalus*, that breeds in Asia, beyond the Himalayas, and winters in numbers in East Africa (Moreau, 1937b, p. 42), while Ali (*in litt.*) informed me of similar migratory behavior in Indian breeding *Merops superciliosus persicus*, *Coracias garrulus semenowi*, and *Muscicapa striata neumanni*.

Before leaving *C. jacobinus*, it is necessary to discuss the melanistic morph of the race *serratus* in connection with its migratory movements. This black phase is frequent in the eastern parts of the breeding range of *serratus*—Natal, Cape Province, Orange Free State, etc., and, like the pale morph, this one is absent from South Africa during the southern winter. These melanistic individuals are, in a sense, critical material, as the pale morphs could not be distinguished from similar birds resident in more tropical areas to which they presumably migrate. Yet, aside from a small number of black-plumaged birds (four), this phase has been conspicuously absent from collections made throughout Africa outside of their southeastern breeding range. The four black-phase birds, indistinguishable from southeast African *serratus*, that have been taken are as follows: At Port Gentil, Gabon (November 3), south of Lake Chad (July), at Kulme, Darfur (July 11), and at Sagon River, Ethiopia (June 4). These pose a very puzzling problem that cannot be completely resolved. These have been discussed briefly in our account of polymorphism (see p. 71) but our interest in them at this point is in their implications concerning their geographic movements. The November Port Gentil, Gabon, specimen, in very fresh plumage, can hardly have been a migrant from southeastern Africa, where at that time of the year *serratus* is breeding. The dates and the respective stages of molt and of feather wear of the other examples do not fit closely the seasonal chronology of the southern birds, and in this respect they suggest that they might be considered as individual (and rare) instances of melanism of the more northern race *pica*. In southeastern Africa *serratus* is dimorphic, and the melanistic phase is common, but if the four northern records of black-phase birds, listed above, are not *serratus*, or, at least, are not unquestionably of that subspecies, it would follow that not a single completely convincing example of the black morph of *serratus* has yet been collected away from its breeding range. There is no inherent

reason why *pica* may not produce an occasional melanistic individual as *serratus* does in such numbers, although breeding examples of such have not been found as yet. If the Gabon, Lake Chad, Darfur, and Ethiopian black examples are looked upon as *pica*, where do the black *serratus* go when they leave their breeding range? If they are *serratus*, why have so few of this phase been collected during the southern winter while so many more of the pied phase have been taken? The discrepancy in numbers of winter specimens of the two is not at all consistent with their numerical status (almost equivalence in some localities) in southeastern Africa during the southern summer. Is it possible that the bulk of eastern *serratus*, which would include most of the black morphs, migrate a relatively short distance into Mozambique, an area where relatively little collecting has been done, and where Lamm (1955, p. 33) found this cuckoo (recorded binomially by him, but almost certainly *serratus*) from December through February? The only evidence, if it may be called that, suggesting that some of the melanistic *serratus* from southeastern Africa may wander far beyond Mozambique, even as far as southern Ethiopia, is that Mearns (in Friedmann, 1930, pp. 272-274) not only collected one bird, already mentioned, at Sagon River, on June 4, but saw four there, June 3 to 6, and two others at Turturo, June 15 to 17. If Mearns was correct in his identification of these sight records, this is the only instance known of a substantial, as opposed to a casual or individual, movement of these dark *serratus*. It is certainly not likely that the breeding *pica* of southern Ethiopia frequently produce melanic morphs in a limited area, or we would have had some other evidence of it by now, and, hence, if these records of Mearns are accepted they must be looked upon as migrant *serratus*. In support of this latter interpretation it may be noted that Mearns collected two examples of the pied plumage phase of *serratus* at Gato River, near Gardula, southern Ethiopia, April 7 to 8, together with other examples of the white-breasted race *pica* (*ibid.*, pp. 268-272). That pied morphs of *serratus* could reach southern Ethiopia as early as April 7 suggests either a very rapid migration, which is not very likely, or that some of the southern birds must start north considerably before others.

In Southern Rhodesia, where we might expect to find the black phase with some regularity either as a breeder or as a migrant, M. P. S. Irwin informs me that he has never seen one in life, and that the collections in Bulawayo contain a single Southern Rhodesian example, taken at Forest Vale, near Bulawayo, on November 20, and another

from Livingstone, Northern Rhodesia, collected on October 19. These, and one other from Nyasaland, are the only black *serratus* out of a series of 64 skins from the Rhodesias and Nyasaland in the collections of the National Museum of Southern Rhodesia. In Nyasaland, Benson (1953, p. 35) noted two reliable sight records of the black-phase *serratus*, one from Fort Johnston in March, the other at Monkey Bay, in November. Benson assumed that these birds were transients in Nyasaland, and called them migrants from the north. I presume this means that they were looked upon as migrants coming from (November) their more northern wintering grounds on their return to their southern breeding area, or (March) returning to the north for the off-season.

To return, in our discussion, to southern Mozambique, Lamm (*cit. supra*) mentioned that in early December he saw both color phases of *Clamator levaillantii*; however, without the specimens (which were not collected), it is impossible to be certain that the black individual was really *levaillantii* and not *serratus*, for the dark morph of the former has not been found south of extreme northeastern Tanganyika. In reply to my inquiry, Lamm has informed me that this sight record was made at Vila Luisa on December 10, 1950. His notebooks record an ". . . all black cuckoo with white wing patch; near it another, black above, white below heavily streaked on the chest, probably a pair . . ."

It may also be mentioned that Pakenham (1948, p. 99) saw a black crested cuckoo in Zanzibar, April 10, which he considered as probably *C. j. serratus*. On the basis of the geographic proximity of Zanzibar to the known range of the black phase of *levaillantii*, Pakenham's bird may have been of this species. The mere sight record, unfortunately cannot be identified, and remains relatively useless.

To summarize, the peripheral populations of the jacobin cuckoo, *serratus*, in Africa south of the Zambezi River, and *pica* in northern India, are highly migratory; typical *jacobinus* of southern India is partly migratory, and *serratus* and *pica* in much of tropical Africa are apparently fairly resident in some places and move about without obvious correlation with season, climate, rainfall, or other noticeable factors in other localities. In large areas of tropical Africa a breeding form and two or more migrant, either transient or "wintering," populations often occur together. The movements of southeastern *serratus*, as evidenced by its melanistic morphs, are still unclear, but there is no question as to their going north during the southern winter.

Clamator levaillantii

As in *C. jacobinus*, the population of the stripe-breasted cuckoo breeding south of the Zambezi leaves that area after the end of the southern summer in late March, and does not return until October. Elsewhere in Africa it has been noted as a local migrant, or at least as a fluctuating element in the avifauna, locally present one day and absent the next. In Nyasaland it has been recorded from early October to May and even to June, and has been known to breed there. It is assumed by Benson (1953) that it migrates to somewhere to the north for the rest of the year. In the Rhodesias, where it also is known to breed, it is also seasonal, although further data are needed, especially from Northern Rhodesia, to clarify the local picture. Thus, in that country the earliest spring date is given as November 8, a month later than in South Africa (!) and the latest autumn date as May 4. Grant and Mackworth-Praed (1952, p. 506) wrote that it passes through Northern Rhodesia in November and December to breed farther south, and concluded that "there is certainly a northern and a southern breeding bird but this is probably not the whole story."

The seemingly haphazard occurrence of the species in localities where it has been found to be present or absent without obvious seasonal correlations, was stressed by Jackson (1938, pp. 497-498) in both Kenya and Uganda, although the species has been recorded there throughout the year. In Tanganyika the picture also is still confusing. Moreau (1937b, p. 23) noted that the only localities in that country where the species had been recorded as breeding were Iringa, from February to March; the east side of Lake Nyasa, in May; at Kilosa, in April. He recorded that it had been seen at Kigoma and at Uvinza in November, when it was molting. He considered it not unlikely that the nonbreeding birds in Kenya and northern Tanganyika may have been migrants from Ethiopian breeding grounds, while the southern Tanganyikan birds ". . . in the east up as far as the Central Line represent a different population breeding there and with their own movements . . ."

In coastal Kenya and the adjacent parts of northeastern Tanganyika, Percival (*in* Bannerman, 1910, p. 704) concluded that the stripe-breasted cuckoo was present as a "visitor" for a matter of only about 6 weeks in the year. However, this is erroneous, as specimens of the local melanistic morph have been taken in that restricted area in every month of the year except July and August, and the present lack of records for those 2 months is not indicative of ab-

sence. Further evidence of the nonmigratory status of this cuckoo in that area is afforded by the fact that during the more than half a century since Percival's work many and very comprehensive collections and observations have been made in practically all parts of Kenya at all times of the year, and not a single example of the black morph (the so-called "*albonotatus*") has ever been collected outside of the coastal strip, except for one very surprising, but apparently acceptably authenticated record, taken by Percival, at 10,000 feet on Mount Kenya. As mentioned in our discussion of polymorphism (pp. 70-75) this last record would seem better interpreted as an unusual local melanism of the population of *C. levaillantii* resident on Mount Kenya, than as a migrant from the coastal lowlands.

In the Republic of the Congo (former Belgian Congo), Chapin (1939, pp. 181-182) treated it as a resident bird in the Uele and in most other lowland savannahs, absent from forested areas, but known to breed in May and October (fledglings taken). Further to the north, in the Sudan, Cave and Macdonald (1955, p. 174) found it to be a common nonbreeding visitor between March and October, while in Darfur Lynes (1925, p. 354) concluded it was a rather infrequent summer visitor to the West Basin. In Mali, according to Malzy (1962, p. 34) the stripe-breasted cuckoo is a local migrant, common at the close of the rainy season, seen at Bamako from July to November.

It is not clear as yet if the species leaves its Ethiopian breeding grounds (where it breeds from June to September) during the northern winter, but it may well do so in the highlands, thereby adding to the confusing population in Kenya to the south and in Sudan to the west. In Eritrea, K. D. Smith (1957, p. 309) called it a "presumed resident" but had only scanty evidence.

The movements of the species in West Africa are still uncertainly known. Bannerman (1933, pp. 108-110) could only say that a "... corresponding movement to those which take place in East Africa certainly occurs in West Africa, but observers being fewer we have less data . . ." He found from his compiled records that it appeared to have been met with only seldom between July and November south of latitude 12°. It is known to breed in Ghana (February) and in Nigeria (July). In the latter country, Marchant (1953, p. 45) found it to be an uncommon transient from December to February. By this he probably meant to infer that it wintered somewhere to the south and bred to the north, but he made no geographic guesses as to how far in each direction its migration extended. The species is

present throughout the year in Gambia, but the local population is increased by migrants in June.

Insofar as it is possible to summarize all these data, we may say that the species is clearly seasonal in Africa south of the Zambezi River; occurs throughout the year in equatorial Africa, where, however, its numbers are swelled during the southern winter months, and where it appears to comprise several populations, each with its own movements. It has not yet been ascertained to breed north of Ethiopia, the Republic of the Congo, Nigeria, Ghana, and Liberia, but probably does so. Inasmuch as it is not possible to separate, taxonomically, any geographic forms of this cuckoo and inasmuch as the known breeding records show a general, although spotty, distribution, it follows that the picture is somewhat like that in *C. jacobinus*, but wholly contained within the African continent.

The species seems to be scarcer now than formerly in the southeastern portion of its range. Thus, in the late years of the 19th century the Woodward (1899) found it at the Umfolozi River, in Zululand, while today Clancey (*in litt.*) informs me that he has never met with it in Natal and considers it a very rare bird in the southern portion of its range. I also never encountered it in Natal, but only in the northern Transvaal (at Moorddrift, in December), where it was breeding. Even where it is common it is usually less numerous than the jacobin, although there is local variation in its numbers. In the Ashanti forest and the northern sections of Ghana, Lowe (1937, p. 635) reported it as abundant and present everywhere in the grass savannahs and in the open clearings in the forest.

Clamator coromandus

This is the one species of the genus that may have no nonmigratory populations or individuals, but available information is insufficient to establish this. The species ranges over an area where there never have been many resident observers and, as a result, our present data depend largely on specimens collected and deposited in museums. I have examined a large number of documented specimens of this cuckoo, and these, together with what has been published, yield the following picture. The species is known to breed in the Himalayan foothills from Garhwal and Nepal east to Assam at elevations of from about 2,000 to 8,500 feet, and in Burma at elevations of from 1,500 to 6,000 feet; north to southeastern China (Kwangsi, Kwangtung, Kiangsi, Fukien, Chekiang, and Hupeh Provinces; possibly

also in Kweichow and Hunan); and southeast (rarely) to northern Thailand (Deignan, 1945, p. 158).

In the nonbreeding season it wanders to Chota Nagpur, Madras, Mysore, and Karala in India, to Ceylon, to Thailand (where it is a transient in spring and autumn, never found in winter), to the entire length of the Malay Peninsula (except the eastern side), the Indo-Chinese countries, Lingga Archipelago, Sumatra, Java, Celebes, and Borneo, and occasionally to the Philippines. In Burma, Smythies (1953, pp. 326-327) considered it a local migrant, but its movements there have not yet been worked out in detail or with any accuracy. Similarly, the seasonal movements of this cuckoo in southeastern China are yet to be defined with precision. Thus the Caldwells (1931, p. 240) considered it only as a migrant in southern Kwangtung, but in the northern portions of that Province they found it a not uncommon resident.

Clamator glandarius

Both the northern and the southern extreme populations of this species are highly and regularly migratory; the individuals breeding in equatorial portions of Africa are assumed (but not proved) to be non-migratory. In South Africa and South-West Africa, north to Southern Rhodesia, Nyasaland, and southern Mozambique, the species is present only from September to March. In its Mediterranean breeding ground, where the seasons are reversed, the great-spotted cuckoo arrives at about the time the southern birds go north. Thus, Stresemann (1928, p. 703) noted that this cuckoo arrives from its tropical African winter quarters as early as the beginning of February in upper Egypt and Morocco, in early April in Gibraltar, and that it leaves again for the south in July and early August, and, in Egypt, even as early as June. He pointed out that there was an obvious correlation between its migration dates and its host requirements. It had to establish itself on its breeding grounds before the prospective hosts began to lay. In northwestern Africa, where the hosts are magpies, whose early egg dates are from late March to early April, and in upper Egypt as soon as there are no new nests of its corvine hosts (the crows are all beyond this stage in June), the cuckoo begins to leave for equatorial Africa. This seems to imply a more hurried departure than is characteristic of the birds breeding south of the Zambezi River. Thus, in Southern Rhodesia, Smithers, *et al.* (1957, p. 67) record it as breeding from October to January, but not leaving for the north until April. Meinertzhagen (1930, pp. 345-347) found

it was absent from August to December in Egypt (not merely upper Egypt); he noted a marked northward passage at Wadi Halfa, Aswan, and Luxor in early February, when groups of from 10 to 20 individuals were seen passing slowly down the Nile Valley. The same author (1954, pp. 306-307) found this cuckoo to be a regular but infrequent migrant in Arabia, considerable numbers going through in late March and April—a rather late date compared with the earlier passages farther west.

In Eritrea, K. D. Smith (1957, p. 308) recorded a definite influx of birds in the coastal plain between December and March. The birds were common in summer (July and August) below 3,000 feet, and were absent from Eritrea in the winter.

Cave and Macdonald (1955, p. 174) considered this cuckoo both a resident and a nonbreeding (wintering) visitor in Sudan, but were unable to say to which of these categories most of the individuals belong. In the Darfur Province, Lynes (1925, pp. 353-354) worked out the local situation in greater detail. He concluded that there were two distinct groups of cuckoos, one composed of individuals that bred farther to the south in equatorial or in southern Africa, and which spent their off-season farther north than Darfur, and merely passed through the area twice a year, and another group of Mediterranean breeding birds that migrated through Darfur in smaller numbers than the southern breeders. The southern breeders passed through Darfur from May until August, reaching their greatest numbers in June and July. Lynes found that these included adults, immature birds, and birds of the year, the last varying from 3 to 6 months in age, but not in molt, while the adult and subadult birds were molting. He further noted that in its middle period the passage was rapid, the birds arriving chiefly very early in the morning after some amount of nocturnal travel, and moving on during the day, lingering only to feed. The migration ended in late July, and no more were seen for 3 months, except for one stray young bird about 4 months old collected on August 20. The Palaearctic breeding migrants passed through Darfur in November and December. Lynes found no resident breeding great-spotted cuckoos in Darfur, but it would seem that further observations may demonstrate that the species breeds there regularly, although perhaps not abundantly. It may be recalled that some years after Lynes did his field studies, Madden (1934 pp. 94-95) saw a young fledgling of this cuckoo being attended by its foster-parents, a pair of the starling, *Lamprotornis caudatus*, at Khuwei, southern Darfur. Farther to the east, at Dembo, near the

Bahr-el-Ghazal, the cuckoo has been reported breeding as well, and also to the west of Darfur, in Mali, where Malzy (1962, p. 34) reported some migrants and some "sedentaires."

Madden's notes from southern Darfur included a very marked northward migration through El Fasher in May and June, apparently of birds that had finished breeding somewhere to the south, and also migrants at Ngala in late June, also apparently of southern birds passing through to spend the off-season somewhere to the north of Darfur.

Farther to the south, in the Kagera Park, in the Republic of the Congo, Curry-Lindahl (1961, p. 270) recorded a migratory influx of these cuckoos January 27 and 28. In Uganda and in Kenya, van Someren and others have put on record observations that add up to a somewhat obscured picture because of the obvious difficulty of differentiating in the field resident from migrant birds. There is an influx of nonbreeding (wintering) visitors from the north, and it is possible that southern breeding birds also reach those areas in the southern winter. Van Someren (1931, p. 24) found that he could distinguish migrants from resident birds, from post-mortems of collected specimens, the migrants usually being very fat, the local residents not so. Birds seen in Kenya after May were mostly resident, which suggests that relatively few individuals from south of the Zambezi River reach Kenya. Jackson (1938, pp. 493-495) was inclined to doubt some of van Someren's statements, but he overlooked the fact that the latter had specifically mentioned fledged juvenal birds in May in Kenya, which must have been locally raised.

A similar situation also appears to occur in Tanganyika, but the total evidence is much scarcer. There is definite evidence of breeding, hence of resident birds, in December at Unyanganyi, and in March at Iringa. In Nyasaland the species occurs from mid-September to mid-March, with the greatest number of birds noted between September and November.

SUMMARY AND CONCLUSIONS

The genus *Clamator* originated in southeastern Africa in Pliocene or pre-Pliocene time, from a primordial stock that appears to have its least changed, current representative in the southern race of *C. jacobinus* (*serratus*). From its original locus it expanded its range over most of sub-Saharan Africa and spread to India and southeast Asia, and thence to the Mediterranean basin as well. In its early northward progression in Africa the original *jacobinus* stock gave

rise to a larger, pectorally heavily striped derivative that became *levaillantii*, and, somewhat later, in southern Asia, to an equally large, red-winged form, the present stock of which is *coromandus*. This last-named group, in turn, gave rise to what developed into *glandarius*, which emigrated westward from northern India to the Near East, Egypt, and to the western portion of the Mediterranean, the Iberian Peninsula, Morocco, and Algeria. Much later this form suddenly expanded its range southward to encompass much of Africa south as far as Cape Province.

The genus evolved very early from a primordial Cuculine stock that was already parasitic in its breeding, but that had not yet developed the evicting behavior in the young or the tendency to host-adaptive variable egg morphism with the concomitant development of host-specific gentes. In the course of its subsequent history *Clamator* never developed either of these features as did the more specialized genus *Cuculus*. Its original eggshell coloration was plain, unmarked white as in *C. jacobinus serratus*, and in this form there is no sign of host selection with species reference to egg similarity. From this was developed a plain bluish or blue-green egg coloration, as still present in the two northern races of *jacobinus*, *pica* and the nominate subspecies, as well as in *levaillantii* and in *coromandus*. In these segments of the genus the choice of fosterers has been arrived at with definite correlation to general egg similarity. Finally, in the most advanced species, *glandarius*, we have a patterned, speckled or blotched, egg coloration superimposed on a pale greenish ground color, and in this case the inference to be derived from the evidence is that it developed together with an early fixation upon magpies as hosts.

In the case of *glandarius*, with its unusually fine egg adaptation toward this host choice, we find evidence that this restriction, both in fosterer and in geographic range, became disadvantageous for the species as a whole, and that a large segment of its population underwent a great geographic emigration, in a way comparable to what in morphological evolution has been termed an "escape from specialization."

The start of this escape from host restriction on a fosterer of very limited sympatry had already begun in eastern Egypt where *Corvus* was utilized in the absence of *Pica*. The *glandarius* population that expanded over much of sub-Saharan Africa was apparently the less perfectly adapted portion of its species in its old Mediterranean homeland, as is still evidenced by the great disparity in host-parasite egg ratios shown in its uncorrelated multiple parasitism in its newer

breeding range. In the course of its rapid spread over this vast *Pica*-allopatric area, it has not altered its eggshell pattern although it has broadened greatly its range of acceptance of host nest types, enabling it to parasitize such divergent fosterers as arboreal, open-nesting corvids and earth-tunnel nesting sturnids. As is pointed out in the present paper, the fact that *glandarius* was parasitic largely on birds of greater size, capable of rearing multiple parasites as well as some of their own young, gave the cuckoo an immunity from selective pressure, but as it increases its use of smaller, sturnid hosts the parasite may find itself affected by this pressure, from which it is relatively protected as yet.

A factor that appears to have been of considerable importance in the advent of the geographic spread that consummated in the emigration to sub-Saharan Africa of the less perfectly adapted portion of the original circum-Mediterranean population of *glandarius* was the shift in the main stress of selective pressures when that original population became numerically high. Until that demographic saturation had been reached, and especially while the species was developing through its adaptive evolution with regard to its primary host, the chief focus of natural selection was between *glandarius* and its environment (including in the latter, its magpie fixation). Once *glandarius* had become successful and numerous, the primary selective pressure was between members of its own kind, and it is this change that seems to have been involved in its geographic "shedding" of those segments that were less able to stand the new orientation of natural selection. This left only the better adapted individuals in the original homeland, which is the reason for the difference still apparent between them and their sub-Saharan emigres.

Another evolutionary trend found in some other groups of brood parasites, a gradual shortening of the incubation period, is absent in *Clamator*. In fact, the meager data available suggest just the opposite, although the more advanced species of the genus, with longer incubation periods, tend to make use of hosts with still longer ones.

To summarize, brood parasitism in *Clamator* has achieved a high degree of adaptive excellence by virtue of a restriction of host choice to birds of generally similar eggs (northern races of *jacobinus*, and *levaillantii*, *coromandus*, and *glandarius*), and only relatively recently has this smoothly functioning correlation been upset by a portion of the membership of the most advanced, most "perfectly" adapted species, *glandarius*. Traces of incipient tendencies toward egg morphism may be detected in *levaillantii*, but they have not developed very far.

The original *Clamator* stock, as represented by *C. jacobinus serratus* had a tendency toward plumage polymorphism, a trend that could, potentially, enhance the process of subsequent differentiation into discrete taxonomic entities. This polymorphism remained localized in the ancestral home—southeastern Africa—although traces of the tendency still occasionally crop up elsewhere in African *jacobinus* and, strangely enough, in a very limited portion of its range, in *levaillantii*. No trace of polymorphism has been found in Asiatic *jacobinus*, in *coromandus*, or in *glandarius*. The lack of evolutionary consequences of this early polymorphism is due to the fact of its neutral nature.

The variations in "normal" plumages show clearly that *levaillantii* was derived from *jacobinus*; the phylogenetically conservative tendency of juvenal plumage characters indicates that *glandarius* arose from a *coromandus*-like stock. The fact that *Clamator*, during its very long existence, has produced only 4 species, as against 12 in the younger *Cuculus*, or 12 in *Chrysococcyx* (including "*Chalcites*"), coupled with the evolutionarily inert nature of its polymorphic trends, suggests that the genus is one that has been relatively less affected by evolutionary change.

Similarly, migratory behavior has remained less completely formulated and less rigid in its manifestations in many sections of the genus, even varying markedly in different segments of individual species. We have noted the entire range of behavior from absence of migration to local migration, to partial migration, to total and regular seasonal mass movements of great geographic extent.

We must remember that, like other organisms, birds, their structures and their habits, do not evolve; they are evolved. The creatures are merely the material on which evolutionary processes exert their influence and on which they leave their marks and it is from a study of these marks that we reconstruct their past history and experience.

Clamator has existed in a less active, more "secluded," evolutionary arena than some other genera of its family. Nonetheless, it has had a long, continuous, and successful history, and in the course of this great duration it has shown an early adaptation in egg coloration to a then new and fairly definite set of host species, and much later, in its climax form, a partial escape from the overly restrictive results of this rigid host specificity. In between these two important incidents in its development, it has pursued a fairly even and relatively uneventful existence, although involving differentiation into four species, each with considerable geographic shifting of stock. This brings out the fact that, in studying a group of organisms, the concept of their

evolution is not completely the same as that of their history. The former should, technically, be limited to the chronology, and, wherever possible, the explanation, of the changes that transpired in the creatures during their history, but should not be considered as the whole of their story, even though it may involve its most salient features. An organism may, and often does, survive environmental changes without undergoing change in itself, as we have seen in the case of *Clamator glandarius*. This is certainly a part of its history, but is hardly something that ordinarily would be considered in an account of its evolution.

APPENDIX

ADDITIONAL HOST DATA

A. DATA ON THE HOSTS OF CLAMATOR GLANDARIUS

So many new species have been added to my original (1949a, pp. 10-15) host catalog and so much additional information has been amassed on some of the others, and so many changes in nomenclature have come about that it seems better to present a new catalog than to attempt to present only the new material with the multitude of cross-references needed to collate them with what was known before. Where the present data suggest no alteration in the earlier statements, they are given very briefly.

Two birds, not in the subjoined catalog, have been mentioned in the literature as hosts, but there is no evidence to support these statements. The North African little owl, *Athene noctua glaux*, has been mentioned as a victim, based on a very indefinite statement by Canon Tristram (1859, p. 77), which may best be ignored. A year later Des Murs (1860, p. 218) wrote that the great-spotted cuckoo laid "without doubt" in the nests of the thrush, *Turdus merula*, but in the more than a century since then no one has reported an actual instance. This statement should also be ignored.

The data on documented hosts are given below.

Falco tinnunculus Linnaeus

Kestrel

Jourdain's single record (1920, p. 72; Friedmann, 1949a, p. 10) has remained unique. The fact that the kestrels were using an old magpie's nest probably was a contributing factor in attracting the attentions of the cuckoo, but it should be mentioned that all the eggs were fresh; in other words, the kestrels were already in occupancy when the cuckoo came there. It suggests that it is the nest itself, rather than the actual appearance of its owners, that is of first im-

portance to the parasite. The record involves the nominate race of the kestrel.

Upupa epops Linnaeus

Hoopoe

Two records of the South African race (*africana*) of this bird as a host of the great-spotted cuckoo have come to my attention. Miss M. Courtenay-Latimer (*in litt.*) found a hoopoe's nest at Bailey Station, eastern Cape Province, on September 9, 1931, containing four eggs of the hoopoe and one of the cuckoo. One of the hoopoe eggs and the cuckoo egg hatched on September 17; two more of the host eggs hatched the next day and the last one on the following day. The young hoopoes remained in the nest for 3 days, when they were found dead and partly devoured by ants nearby. Their actual removal from the nest was not observed, so it is not possible to state whether they were evicted by the young parasite or had died and were removed by their parents. The cuckoo chick remained in the nest for 4 weeks, and the foster-parents were seen feeding it after it fledged, until it flew strongly.

A few years later, near Tregarthens Folly, Cape Province, Miss Courtenay-Latimer saw a hoopoe feeding a fledgling great-spotted cuckoo on November 7, 12, 15, and 20, 1934. The fact that this parent-young relationship was observed on numerous days shows it was not a casual, temporary interest of a food-laden adult in a clamorous fledgling from another bird's nest, and also indicates a duration of postfledging feeding of at least 2 weeks. The first record, entailing an egg of the parasite on September 9, must be one of the earliest egg dates for this cuckoo in South Africa.

The hoopoe has never been found to be parasitized in Europe, but Meinertzhagen (1948, p. 563) noted a single cuckoo apparently closely associated with a hoopoe in Ushant, Brittany, on April 16, 1947. Meinertzhagen did not imply parasitism or any other reason for the observed association and did not even state if the cuckoo was a young bird. If not for Miss Courtenay-Latimer's observation on the South African race of the hoopoe, no one would have suspected any host-parasite situation in Meinertzhagen's terse report. Indeed, as written, it affords no basis for any such interpretation, but the question does arise.

Geocolaptes olivaceus (Gmelin)

Ground Woodpecker

At Waverly Haasfontein, eastern Cape Province, on October 5, 1952, Miss M. Courtenay-Latimer (*in litt.*) observed a ground wood-

pecker feeding a fledgling great-spotted cuckoo about a week out of the nest. This is the only record known to me of this woodpecker as a host.

Corvus corone Linnaeus

Hooded Crow

Two races of this crow have been found to be victimized by the great-spotted cuckoo, the nominate form in southern Spain (one record, now in the British Museum) and the race *sardonius* in Israel and in Egypt. In the last-named country the hooded crow is the chief, if not the invariable, host, and, in all, over 50 Egyptian instances have come to my attention. The numerical relations between host and parasite eggs there are shown in our graph (fig. 10, p. 43), which gives a picture quite different from that of other crows south of the Sahara.

Corvus ruficollis Lesson

Brown-necked Raven

According to Archer (in Archer and Godman, 1961, vol. 3, pp. 649-659) the local race (*edithae*) of this bird is the chief host of the great-spotted cuckoo in former British Somaliland (now part of the Somali Republic). He gave data on five instances from his fieldwork in that area, the actual localities being Arori Plain, Burao, Baraad, and Oadweina. Two other parasitized nests were collected by M. E. W. North, at Brava, former Italian Somaliland (now part of the Somali Republic), and sent to the Coryndon Museum. I am indebted to J. G. Williams for information about them. Belcher (1949, p. 37) reported another parasitized nest near Gabredarre, Ogaden, former Italian Somaliland (now a part of the Somali Republic). In this case, the nest contained a nestling of the host in addition to eggs of its own and of the parasite.

Corvus corax Linnaeus

Raven

Hartert (1912, p. 956) recorded this bird (typical race) as a host of the great-spotted cuckoo in Spain, but the basis for this statement is not given; Valverde (1953, p. 294) notes it as found by Lord Lilford at Aranjuez. It remains a unique record. The only parasitized set of eggs of any species of *Corvus* from Spain that I know of is a set of *Corvus corone* in the British Museum.

Corvus albus Müller

Pied Crow

The number of records of this crow as a victim of the great-spotted cuckoo has been more than doubled since my first (1949a, pp. 11-12)

account. I have data on 18 such cases, from South Africa, Southern Rhodesia, Nyasaland, Tanganyika, and Nigeria. The number of cuckoo eggs per nest varied from 1 to 13, the majority of nests having from 1 to 5 of the parasitic eggs.

Corvus capensis Lichtenstein

Cape Rook

This rook, unique among crows in that it lays pinkish, and not greenish, eggs, with which the eggs of the cuckoo contrast markedly in coloration, is known to be imposed upon in South Africa and Southern Rhodesia (nominate race) and in former British Somaliland (race *kordofanicus*). Of the southern race, there are 13 records in my files; of *kordofanicus*, 2 records (both *ex* Archer and Godman, 1961, vol. 3, p. 657). Five of the southern records are given in my earlier reports (1949a, p. 12; 1949b, p. 514). The additional eight are as follows: five are from Southern Rhodesia (Beatrice, Banket, Salisbury, and Selukwe) and three from eastern Cape Province, South Africa. The number of cuckoo eggs in these sets varies from one to four; in six instances there was a single egg of the parasite with from one to four eggs of the host; in seven nests each had two eggs of the cuckoo with from one to three of the host; one nest had three cuckoo and five rook eggs, and one nest contained four eggs of the parasite and five of the host.

Since the above was written, Pitman (1962, p. 23) has recorded that as many as nine eggs of the cuckoo have been found in a single nest of a Cape rook in South Africa. The exact data on this nest were not presented.

Corvus rhipidurus Hartert

Fan-tailed Raven

As I mentioned in my first account (1949a, pp. 12-13), Lort Phillips and his party found in 1885 that in northern former Italian Somaliland (now a part of the Somali Republic) nearly all of the examined nests of this bird contained eggs of the great-spotted cuckoo, and that in one nest there were no fewer than eight eggs of the parasite with four of the raven. Archer (*in* Archer and Godman, 1961, p. 657) recorded two parasitized nests found in former British Somaliland (now a part of the Somali Republic), one at Sheikh and one at Ariarleh, the former with three eggs of the raven and two of the cuckoo, the latter with one of the host and four of the parasite.

Archer found the brown-necked raven, *Corvus ruficollis edithae*, to be the most frequently used host in the Somali Republic, and in his discussion he appears to include Lort Phillips's data as pertaining to

that species and not to *rhypidurus*. In this he was in error. The Phillips party was in the field from the end of December until the beginning of April, so all the cases of parasitism they observed must have come between these dates. Archer's dates for parasitism on *edithae* were all later, April 29 to June 9, as stated in our discussion of that bird.

***Corvultur albicollis* (Latham)**

White-necked Raven

This species was added to the known hosts of the great-spotted cuckoo by McLachlan and Liversidge, in their revision of Roberts' "Birds of South Africa" (1957). No details were given; it was merely listed as a host.

***Cyanopica cyanus* Pallas**

Azure-winged Magpie

The subspecies *cooki* of this magpie is a frequent victim of the great-spotted cuckoo in Portugal and Spain. All in all, I have learned of some 11 instances of parasitism on this bird, an increase of 4 over those listed in my earlier account (1949a, pp. 13-14).

***Pica pica* (Linnaeus)**

Magpie

The magpie is the primary, almost the exclusive, host of the great-spotted cuckoo in the limited portions of the ranges of the two species where they are sympatric. It is also the one host to which the egg coloration of the parasite is unusually finely adapted. All in all, counting nests with eggs, nests with young, and cases of magpies attendant upon fledgling cuckoos, over 80 instances of parasitism on this host have come to my attention. Geographically they range from Spain, southern France (Arles), northwestern Africa (Morocco, Tunis, Algeria), and Cyprus, to Turkey (Ankara), and Asia Minor.

Five subspecies of the magpie are involved in these records: *melanotos* in the Iberian Peninsula, *pica* in Asia Minor, *bactriana* in Iraq, *galliae* in southern France, and *mauritanica* in northwest Africa. The graph (fig. 12, p. 45) illustrating our present account of "intensity of parasitism" shows the frequency of multiple eggs of the cuckoo in nests of the magpie. This is based on egg records only and does not include cases involving nestlings or fledglings.

The most recent study of the host-parasite relations of the magpie is that of Mountfort (1958, pp. 54-56), whose fieldwork was done in Spain. He found both birds were very common, and that in spite

of heavy parasitism the magpies seemed to be thriving. He and his party found some 50 occupied nests in 1956. That there is some variation in the demographic relations of the two species is suggested by Wadley's notes (1951, p. 75) made in central Anatolia, in Asiatic Turkey. He found that the great-spotted cuckoo was well distributed there, but the total population was quite small, although the magpie was numerous throughout.

Mountfort's experience seemed to indicate that parasitism was generally fatal to the magpie eggs and young, as he wrote that ". . . in only one nest did we ever find the young of both species together, and this was only a very brief period. The nest in question at one time contained three eggs of each species, two of those of the Magpie being dented. The remaining Magpie egg hatched three days after those of the Great-Spotted Cuckoo. Two days later the nestling Magpie had disappeared, presumably having been either smothered or starved. Herein lay the crux of the matter, for the incubation period of the Great-Spotted Cuckoo is only fourteen days whereas that of the much larger Magpie is seventeen to eighteen days. Unless therefore the young Magpies can hatch out from eggs laid well in advance of those of the parasite, they can have no hope of survival . . ."

Garrulus glandarius (Linnaeus)

Common Jay

In my earlier account (1949a, p. 15) I mentioned that Tristram (1866, p. 282) considered it probable that this jay was parasitized in Palestine, but he listed no actual records. Yet, on this basis, several authors have repeatedly referred to this jay as a fosterer of the cuckoo. Since then, Makatsch (1955, p. 152) definitely reported two parasitized nests of the jay in Asia Minor, of the subspecies, *G. g. krynicki*, collected by Krüper, one on May 9, 1882, and the other on May 6, 1901. Each had an egg of the great-spotted cuckoo. I am not aware of any other instances of parasitism on this jay.

Ptilostomus afer (Linnaeus)

Piapiac

Recorded without data, as a victim of the great-spotted cuckoo, by Mackworth-Praed and Grant (1952, p. 505).

Acridotheres tristis tristis (Linnaeus)

Common Mynah

This mynah, introduced into South Africa, has recently been found to be parasitized by the great-spotted cuckoo at Estcourt, Natal, where Godfrey Symons (1962, p. 343) observed a parasitized nest, containing four eggs of the mynah and one of the parasite.

Onychognathus morio (Linnaeus)**Red-winged Starling**

In my first account (1949a, p. 14) I listed three records; since then I have learned of six more. The additional cases make it clear that the red-winged starling must be looked upon as a regular victim of the great-spotted cuckoo in eastern South Africa. Elsewhere in its range this starling has not yet been found to be parasitized.

Spreo bicolor (Gmelin)**Pied Starling**

The statement in my earlier account (1949a, p. 14) may be amplified as I now have data on many more instances of parasitism on this starling. It is the most frequently reported fosterer in eastern South Africa, and is the only earth-tunnel nester regularly and frequently used by the parasite. As many as six cuckoo eggs have been taken from one nest of this bird. The graph (fig. 13, p. 46) illustrating the discussion of "intensity of parasitism" shows the relationship in egg numbers of starling and cuckoo in 14 instances.

Spreo albicapillus Blyth**White-capped Starling**

This starling was added to the known hosts of the cuckoo by Archer (*in* Archer and Godman, 1961, p. 657), who found, at Sheikh, in former British Somaliland (now a part of the Somali Republic), on May 14, a nest of this bird containing two eggs of the parasite in addition to five of the host.

Lamprotornis nitens (Linnaeus)**Red-shouldered Glossy Starling**

Three additional cases have been forthcoming from Natal since the four (not three as erroneously recorded) cases mentioned in my earlier account (1949a, p. 14). All refer to the host race *L. n. phoenicopterus*.

Lamprotornis caudatus (St. Müll.)**Long-tailed Glossy Starling**

At El Obeid, Kordofan, Sudan, in November 1932, Madden (1934, p. 94) noted a pair of long-tailed starlings feeding a recently fledged great-spotted cuckoo. This is still the only record for this host. When I first commented on this case (1956, p. 378) it was the only instance of a hole-nesting bird being parasitized by this cuckoo north of South Africa. Since then, a similar case, involving another, but allied, species of starling, has been reported from former British Somaliland (now a part of the Somali Republic), and still another from Southern Rhodesia.

Lamprotornis chalybeus (Hemprich and Ehrenberg)

Blue-eared Glossy Starling

Two races of this starling have been recorded as victims of the great-spotted cuckoo, *cyaniventris* in the Somali Republic, and *sycobius* in Southern Rhodesia. In former British Somaliland (now a part of the Somali Republic), Archer (*in* Archer and Godman, vol. 3, 1961, p. 657) found a nest at Sheikh, on May 26, containing one egg of the starling and two of the parasite. It is the only record that has come to my notice for the race *cyaniventris*.

The southern race, *sycobius*, was added to the known fosterers of the great-spotted cuckoo by Meyer (1959, p. 85), who found a nest near Que Que, Southern Rhodesia, on November 15, 1958, which contained a young cuckoo, still devoid of feathers, but with the quills just appearing on the tail and wings, a young starling, fully feathered, about 10 to 14 days old, a dead young starling, and a broken, unhatched starling egg. Three days later the two nestlings were still there, but on the following day the young cuckoo was the sole occupant and remained there for another week, when it fledged and was seen attended by its foster-parents.

B. DATA ON ADDITIONAL HOSTS OF CLAMATOR JACOBINUS

Since my first host catalog, a number of additions have been sent to me or have appeared in print. These records, with their pertinent documentation, are here reported. While these species are additions to the earlier catalog they are all infrequently used fosterers, as might be assumed from the fact that they have only recently been so recorded. They all come from Africa, where the chief hosts, bulbuls of the genus *Pycnonotus* and shrikes of the genus *Lanius*, have been reported in this capacity so many times since the last (Friedmann, 1949a) catalog as to leave no doubt as to their primary role in the economy of the pied crested cuckoo.

Centropus grillii Hartlaub

Black-bellied Coucal

A coucal is an unusual host as it builds a fairly domed-over nest on the ground, a site not usually favored by the pied cuckoo. The one known record comes to me from Dr. Johan Ottow (*in litt.*), who has in his collection a parasitized set of the present coucal species, taken at Baviaans Krantz, near Rustenberg, Transvaal, November 30, 1952. The set contained one egg of the host and one of the parasite. The record refers to the race *wahlbergi* of the coucal and *serratus* of the jacobin cuckoo.

Dicrurus adsimilis (Bechstein)**Glossy-backed Drongo**

In my earlier account (1949a, p. 35) I knew of only one old record of Bowker's, quoted by Layard (1877), which was considered questionable. This record remained unique until 1962, when Skead (1962, pp. 72-73) found a parasitized nest in which the drongos successfully reared a jacobin cuckoo. The nominate race of the drongo, and the race *serratus* of the parasite are here involved.

Turdoides jardineii (Smith)**Arrow-marked Babbler**

This babbler, a very frequent fosterer of the stripe-breasted cuckoo, *Clamator levaillantii*, has been listed as a host of the jacobin as well in Northern Rhodesia, by Benson and White (1957, p. 43). On geographic grounds this would involve the host race *T. j. natalensis*.

Terpsiphone viridis (St. Müll.)**Paradise Flycatcher**

Skead (1955, p. 46) found a nest of the paradise flycatcher with an egg of *C. jacobinus* at Fleet Dutch Kloof, King William's Town, eastern Cape Province, December 18, 1954. This is the only instance known to me of the pied cuckoo laying in the nest of this species. This flycatcher is one of the smallest victims yet recorded. The record refers to the race *perspicillata* of the host, and the race *serratus* of the parasite.

Sphenoeacus afer (Gmelin)**Grass Bird**

In my 1956 discussion (p. 379) I mentioned that I saw a parasitized set of eggs of this bird, taken at Inyanga, Southern Rhodesia, by E. F. Allen, in the Victoria Memorial Museum, Salisbury. This is still the only real record, but I have been informed of one other indefinite one since then, also in the general region of Salisbury. The record refers to the race *transvaalensis* of the host and *serratus* of the parasite. This is one of the few birds nesting on, or close to, the ground that are occasionally parasitized.

Motacilla aguimp Dumont**Pied Wagtail**

The African pied wagtail was added to the known hosts of the pied crested cuckoo by van Someren (1956, p. 236) who found it to be imposed upon by no less than three species of cuckoos in the Ngong area, near Nairobi, Kenya; the present one, the solitary cuckoo,

and the didric cuckoo. The lone record involving the jacobin cuckoo refers to the race *vidua* of the host, and *pica* of the parasite.

Telophorus zeylonus (Linnaeus)

Bakbakiri

Additional instances of parasitism on this shrike by the jacobin cuckoo bring the total number of cases known to me up to seven, and make it clear that this bird is a fairly frequent and regular host choice. Of the seven records, six refer to the nominate race of the host, one of the grayish, western race *phanus*.

C. DATA ON ADDITIONAL HOSTS OF CLAMATOR LEVAILLANTII

The stripe-breasted cuckoo is still less often observed, and hence less completely known, than *jacobinus* or *glandarius*. Observations since my 1949 host catalog have served chiefly to emphasize the fact that babblers of the genus *Turdoides* form the main reliance of this cuckoo. Not only have numerous attitional instances of parasitism on the arrow-marked babbler, *T. jardinei*, come to hand, but also two more species of the same genus have been found to be parasitized. A single record of parasitism on a coly has also come to my attention, but this bird is at best only an irregular or a very occasional victim.

On the whole, *C. levillantii*, in its host choice resembles the Asiatic population of *C. jacobinus*, but, as far as present data indicate, is more generally restricted to species of *Turdoides*.

One observation on the chief host, *Turdoides jardinei*, calls for mention here. Jubb (1952, p. 162) watched a fledgling stripe-breasted cuckoo with a family group of arrow-marked babblers and wrote that the young parasite "... was able to imitate the chatter so characteristic of babblers on the wing ...". This would imply some vocal adaptation to a host species, such as Nicolai (1961) has suggested in some of the parasitic *Viduinæ*. In both cases the suggestion needs further support before it may be appraised.

Colius striatus Gmelin

Speckled Coly

One record of this coly as a fosterer of the stripe-breasted cuckoo has been reported. White and Winterbottom (1949) noted that an egg of this cuckoo was found in a coly nest at Ndola, Northern Rhodesia, in December, by Hudson. This coly has also been found to be victimized very occasionally by the jacobin cuckoo, but it is not a regular host to either species. The typical race of the coly is involved in the present record.

Turdoides plebeja (Cretzschmar)**Brown Babbler**

In Gambia, Ross A. J. Walton collected two parasitized nests of the brown babbler (local race *T. p. platycircus*) at Kambo, North Bank Division; one on April 30, 1945, with one egg each of the babbler and the cuckoo, and the other on July 4, 1945, with three eggs of the host and one of the parasite. The Adamawa race of this babbler, *T. p. gularis*, had been known earlier to be parasitized in Nigeria. Both sets of eggs were acquired for his collection by R. Kreuger of Helsinki, to whom I am indebted for the data. The set taken on April 30 has since gone to the collection of Dr. Johan Ottow, who informed me (*in litt.*) that the locality on his set was given as Churchill Town, St. Mary, Gambia.

Turdoides reinwardii (Swainson)**Blackcap Babbler**

R. Kreuger of Helsinki (*in litt.*) informed me that he received from Ross A. G. Walton, a set of one egg of this babbler with one of the stripe-breasted cuckoo, taken at Kambo, North Bank Division, Gambia, on May 1, 1944. This is the only instance I know of this babbler as a host. The record refers to the nominate race.

BIBLIOGRAPHY

AHARONI, J.

1932. Bemerkungen und Ergänzungen zu R. Meinertzhagen's Werk "Nicol's Birds of Egypt." Journ. f. Ornith., vol. 80, pp. 416-424.

ALEXANDER, BOYD.

1900. An ornithological expedition to the Zambezi River. Ibis, ser. 7, vol. 6, pp. 70-109.

ALI, SALIM A.

1927. The Moghul emperors of India as naturalists and sportsmen. Pt. II. Journ. Bombay Nat. Hist. Soc., vol. 32, pp. 34-63.
1931a. The origin of mimicry in cuckoos' eggs. Journ. Bombay Nat. Hist. Soc., vol. 34, pp. 1067-1070.
1931b. Notes on the pied crested cuckoo (*Clamator jacobinus*) in the Alibag Taluka (Kolaba District). Journ. Bombay Nat. Hist. Soc., vol. 34, pp. 1071-1072.
1934. The Hyderabad State ornithological survey. Pt. IV. Journ. Bombay Nat. Hist. Soc., vol. 37, pp. 124-142.
1953. The birds of Travancore and Cochin. Bombay, 436 pp., 22 pls.
1955. The birds of Gujarat. Pt. II. Journ. Bombay Nat. Hist. Soc., vol. 52, pp. 735-802.

ALLEN, GLOVER MORRILL.

1930. The birds of Liberia. Report of the Harvard African Expedition to the African Republic of Liberia and the Belgian Congo, vol. 2, pp. 636-748.

ALLEN, S. STAFFORD.

1863. Letter to editor. Ibis, vol. 5, pp. 363-364.

ALLOUSE, BASHIR E.

1953. The avifauna of Iraq. Publ. No. 3, Iraq Nat. Hist. Mus., 163 pp.

AMADON, DEAN.

1947. Ecology and the evolution of some Hawaiian birds. *Evolution*, vol. 1, pp. 63-68.
1950. The Hawaiian honeycreepers (Aves, Drepaniidae). *Bull. Amer. Mus. Nat. Hist.*, vol. 95, pp. 151-262.

ANDERSSON, CARL JOHAN.

1872. Notes on the birds of Damara Land and the adjacent countries of South-West Africa. London, xlviii + 394 pp., 4 pls.

ANONYMOUS.

1961. *Miscellanea*. *Oolog. Rec.*, vol. 35, p. 31.

ARCHER, GEOFFREY, and GODMAN, EVA M.

1961. The birds of British Somaliland and the Gulf of Aden. Vol. 3, pp. 628-1042, 7 pls.; vol. 4, pp. 1045-1570, 7 pls.

ASHTON-JOHNSON, J. F. R.

1961. Notes on the breeding birds of Cyprus. Pt. II. *Oolog. Rec.*, vol. 35, pp. 17-22.

BAKER, EDWARD CHARLES STUART.

- 1906-07. The oology of Indian parasitic cuckoos. *Journ. Bombay Nat. Hist. Soc.*, vol. 17, pp. 72-83, 351-374, 678-696.
1907. Additional cuckoo notes. *Journ. Bombay Nat. Hist. Soc.*, vol. 17, pp. 876-894.
1913. The evolution of adaptation in parasitic cuckoos' eggs. *Ibis*, ser. 10, vol. 1, pp. 384-398.
1921-22. Cuckoos. Some theories about the birds and their eggs. *Bull. Brit. Ornith. Club*, vol. 42, pp. 93-112.
1923. Cuckoos' eggs and evolution. *Proc. Zool. Soc. London*, No. 19, pp. 277-294.
1927. The fauna of British India including Ceylon and Burma. *Birds*. Vol. 4, 2d ed., London, 471 pp.
1934. Nidification of the birds of the Indian empire. Vol. 3 (Ploceidae-Asionidae), London, 568 pp.
1942. Cuckoo problems. London, 207 pp.

BAKER, H. R., and INGLIS, CHARLES M.

1930. The birds of southern India including Madras, Malabar, Travancore, Cochin, Coorg, and Mysore. Madras, 504 pp.

BALDAMUS, AUGUST CARL EDUARD.

1892. Das Leben der europaischer Kuckucke. Nebst Beiträgen zur Lebenskunde der übrigen parasitischen Kuckucke und Stärlinge. 224 pp.

BANGS, OUTRAM, and LOVERIDGE, ARTHUR.

1933. Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. III. Birds. *Bull. Mus. Comp. Zool.*, vol. 75, No. 3, pp. 143-221.

BANNERMAN, DAVID ARMITAGE.

1910. On a collection of birds made by Mr. A. B. Percival in British East Africa. With field-notes by the collector. *Ibis*, ser. 9, vol. 4, pp. 676-710.

1912. On a collection of birds made by Mr. Willoughby E. Lowe on the West Coast of Africa and outlying islands; with field notes by the collector. *Ibis*, ser. 9, vol. 6, pp. 219-268.
1921. A systematic list of the birds of Sierra Leone. *Ibis*, ser. 11, vol. 3, pp. 283-302.
1922. The birds of Southern Nigeria, Pt. 2. *Rev. Zool. Africaine*, vol. 10, fasc. 2, pp. 88-208.
1923. Report on the birds collected during the British Museum expedition to the Ivory Coast (French West Africa). *Ibis*, ser. 11, vol. 5, pp. 667-748.
1933. The birds of tropical west Africa. Vol. 3, London, 487 pp., 12 pls.
1953. The birds of west and equatorial Africa. 2 vols., London, 1,526 pp., 54 pls., 433 text figs.
1955. The birds of the British Isles. Vol. 4, Edinburgh, 257 pp.
- BANNERMAN, DAVID A., and BANNERMAN, W. M.
1956. Birds of Cyprus. Edinburgh, 384 pp.
- BARTELS, MAX.
1910. Zu Dr. C. Parrot's "Beiträge zur Ornithologie Sumatras und der Insel Banka." *Journ. f. Ornith.*, vol. 58, pp. 484-488.
- BATES, GEORGE LATIMER.
1930. Handbook of the birds of West Africa. London, xxiii + 572 pp., 2 maps.
- BATES, R. S. P.
1938. On the parasitic habits of the pied crested cuckoo [*Clamator jacobinus* (Bodd.)]. *Journ. Bombay Nat. Hist. Soc.*, vol. 40, p. 125.
- BATES, R. S. P., and LOWTHER, E. H. N.
1952. The breeding birds of Kashmir. Oxford University Press, 368 pp., 5 pls.
- BEDDARD, FRANK E.
1885. On the structural characters and classification of the cuckoos. *Proc. Zool. Soc. London*, pp. 168-187.
- BÉDÉ, PAUL.
1926. Notes sur l'ornithologie du Maroc. *Mem. Soc. Sci. Nat. Maroc*, No. 16, pp. 25-150.
- BELCHER, CHARLES FRANCIS.
1930. The birds of Nyasaland. London, xii + 356 pp., 1 map.
1949. Eggs from Somalia. *Oolog. Rec.*, vol. 23, pp. 35-41.
1950. Notes on some eggs collected in northern Nyasaland. *Oolog. Rec.*, vol. 24, pp. 2-10.
- BENSON, CONSTANTINE WALTER.
1940. Further notes on Nyasaland birds. Pt. II. *Ibis*, ser. 14, vol. 4, pp. 387-433.
1945. Notes on the birds of southern Abyssinia. Pt. 2. *Ibis*, vol. 87, pp. 488-509.
1953. A check list of the birds of Nyasaland. Blantyre, vi + 118 pp., 1 map.
- BENSON, CONSTANTINE WALTER, and PITMAN, C. R. S.
1956. Some breeding records from Northern Rhodesia. Pt. II. *Oolog. Rec.*, vol. 30, pp. 21-27.

- BENSON, CONSTANTINE WALTER, and WHITE, CHARLES MATTHEW NEWTON.
1957. Check-list of the birds of Northern Rhodesia. Lusaka, 166 pp., 28 pls., 1 map.
- BERGER, ANDREW J.
1960. Some anatomical characters of the Cuculidae and the Musophagidae. Wilson Bull., vol. 72, No. 1, pp. 60-104.
- BERLIOZ, M. JACQUES.
1934. Étude d'une collection d'Oiseaux du Tchad (A. E. F.). Bull. Mus. Hist. Nat. Paris, 2d ser., vol. 6, No. 6, pp. 490-496.
- BISWAS, BISWAMOY.
1960. The birds of Nepal. Pt. 2. Journ. Bombay Nat. Hist. Soc., vol. 57, pp. 516-546.
- BLANCHET, ALFRED.
1955. Les Oiseaux de Tunisie. Memoires de la Soc. des Sci. Nat. de Tunisie, No. 3, 84 pp.
- BLANFORD, WILLIAM THOMAS.
1870. Observations on the geology and zoology of Abyssinia made . . . in 1867-68. London, xii + 487 pp. 13 pls.
1876. Eastern Persia. An account of the journeys of the Persian Boundary Commission, 1870-71-72. Vol. 2, Zoology and Geology, 516 pp. 28 pls. London.
- BOGERT, CARDINE.
1937. Birds collected during the Whitney South Sea Expedition, XXXIV. The distribution and the migration of the long-tailed cuckoo (*Urodynamis taitensis* Sparrman). Amer. Mus. Novitates, No. 933, pp. 1-12.
- BOUET, GEORGES.
1961. Faune tropicale. XVII. Oiseaux de l'Afrique tropicale (Pt. 2), pp. 421-798.
- BOXBERGER, LEO VON.
1927. Zur fortpflanzung indischer Kuckucksarten. Beitr. z. Fortpflanzungsbiol. d. Vogel, vol. 3, pp. 24-25.
- BRADFIELD, R. D.
1931. The crested cuckoos of South Africa. Ostrich, vol. 2, pp. 7-9.
- BRAUN, FRITZ.
1908. Unsere kenntnis der Ornithologie der Kleinasiatischen Westküste. Journ. f. Ornith., vol. 56, pp. 539-629.
- BREHM, A. E.
1853. Zur Fortpflanzungsgeschichte des *Cuculus glandarius*. Journ. f. Ornith., vol. I, pp. 144-145.
1861. Noch einmal das Brutgeschäft von *Oxylophus glandarius*. Journ. f. Ornith., vol. 9, pp. 392-394.
- BRELSFORD, W. VERNON.
1942. Migration notes, Chinsali, Northern Rhodesia. Ostrich, vol. 13, pp. 38-41.
- BROEKHUYSEN, G. J.
1956. Occurrence and movement of migratory species in Rhodesia and southern Africa during the period 1950-1953. Pt. II. Ostrich, vol. 27, pp. 159-167.

BROMLEY, F. C.

1952. Short records and notes. *Ostrich*, vol. 23, pp. 131-132.

BROSSET, A.

1956. Les oiseaux du Maroc oriental de la Méditerranée à Berguent. *Alauda*, vol. 24, pp. 161-205.

BROWN, LESLIE H.

1948. Notes on birds of the Kabba, Ilorin and N. Benin provinces of Nigeria. *Ibis*, vol. 90, No. 4, pp. 525-538.

BRUNEL, J.

1958. Observations sur les oiseaux du Bas Dahomey. *L'Oiseau et Rev. Française d'Ornith.*, vol. 28, pp. 1-38.

BUCKNILL, JOHN A.

1908. A description of some portion of the oological collection of South African birds' eggs in the Transvaal Museum, Praetoria. *Journ. S. Afr. Ornith. Union*, vol. 4, pp. 69-102.

BUTLER, ARTHUR LENNOX.

1908. A second contribution to the ornithology of the Egyptian Soudan. *Ibis*, ser. 9, vol. 2, pp. 205-263.

CABANIS, JEAN.

1878. Uebersicht der Vögel Ost-Afrikas, welche von den Herren J. M. Hildebrandt und v. Kalckreuth gesammelt sind. *Journ. f. Ornith.*, vol. 26, pp. 213-246.

CALDER, DAVID R.

1962. Colour of cuckoo eggs. *African Wild Life*, vol. 16, No. 4, p. 344.

CALDWELL, HARRY R., and CALDWELL, JOHN C.

1931. South China birds. Shanghai, 447 pp.

CAMPBELL, LOUIS W.

1948. Nest-building adaptability of the eastern red-wing. *Wilson Bull.*, vol. 60, p. 244.

ČAPEK, V.

1896. Beiträge zur Fortpflanzungsgeschichte des Kuckucks. *Ornith. Jahrbuch*, vol. 7, pp. 41-72, 102-117, 146-157, 165-183.

CARPENTER, C. J.

1933. Contribution à l'étude d'ornithologie Marocaine. *Les Oiseaux du Pays Zaïan. Bull. Soc. Sci. Nat. du Maroc*, vol. 13, pp. 23-68.

CARTER, G. S.

1954. Animal evolution, a study of recent views of its causes. *Rev. ed.* London, 368 pp.

CAVE, FRANCIS O., and MACDONALD, J. D.

1955. The birds of the Sudan. Edinburgh, 442 pp., 24 pls., 2 maps.

CHAMBERS, W. J.

1863. Letter to the editor. *Ibis*, vol. 5, pp. 474-475.

CHAPIN, JAMES PAUL.

1923. Ecological aspects of bird distribution in tropical Africa. *Amer. Naturalist*, vol. 57, pp. 106-125.

1939. The birds of the Belgian Congo. Part II. *Bull. Amer. Mus. Nat. Hist.*, vol. 75, 632 pp.

1953. The birds of the Belgian Congo. Part III. *Bull. Amer. Mus. Nat. Hist.*, vol. 75A, 821 pp.

1954. The birds of the Belgian Congo. Part IV. *Bull. Amer. Mus. Nat. Hist.*, vol. 75B, 846 pp., 27 pls., 45 text figs.

CHUBB, E. C.

1914. A descriptive list of the Millar collection of South African birds' eggs. *Annals Durban Mus.*, vol. 1, pt. 1, pp. 29-106.

CLANCEY, PHILIP A.

1951. Notes on birds of the South African subcontinent. *Annals Natal Mus.*, vol. 12, pt. 1, pp. 137-151.
1960. Miscellaneous taxonomic notes on African birds. XV.4. The races of the jacobin crested cuckoo *Clamator jacobinus* (Boddaert) occurring in Africa south of the Zambesi River. *Durban Museum Novitates*, vol. 6, pt. 2, pp. 27-31.

COCHRANE, J. H.

1863. Letter to editor. *Ibis*, vol. 5, pp. 361-363.

COTT, HUGH B.

1940. Adaptive coloration in animals. London, 508 pp., 49 pls.
1954. Allaesthetic selection and its evolutionary aspects. *In* *Evolution as a process*. Ed. by J. S. Huxley, A. C. Hardy, and E. B. Ford. Pp. 47-70.

CURRIE, A. J.

1916. The birds of Lahore and the vicinity. *Journ. Bombay Nat. Hist. Soc.*, vol. 24, pp. 561-577.

CURRY-LINDAHL, KAI.

1960. Ecological studies on mammals, birds, reptiles and amphibians in the eastern Belgian Congo. Part II. *Annales du Musée Royal du Congo Belge Tervuren (Belgique)*, ser. 8, zool., vol. 87, 170 pp., 20 pls.
1961. Exploration du Parc National Albert et du Parc National de la Kagera. II. Mission K. Curry-Lindahl (1951-1952, 1958-1959), fasc. 1, 331 pp., 22 pls.

DARLINGTON, C. D.

1953. *The facts of life*. London, 467 pp.

DARLINGTON, PHILIP J., JR.

1957. *Zoogeography; the geographic distribution of animals*. New York, 675 pp.

DAVIES, C. J.

1911. Notes on the birds of the District of Matatiele, East Griqualand. *Journ. S. Afr. Ornith. Union*, vol. 7, pp. 23-48.

DE BEER, GAVIN R.

1940. *Embryos and ancestors*. Oxford University Press, 108 pp.

DEIGNAN, HERBERT GIRTON.

1945. The birds of northern Thailand. *U.S. Nat. Mus., Bull.* 186. 616 pp., 9 pls., 4 maps.

DE KLERK, W. DE K.

1942. Notes on nests of birds in Adelaide, Cape Province. *Ostrich*, vol. 13, pp. 57-63.

DES MURS, O.

1860. *Traité général d'ologie ornithologique . . . au point de vue de la classification*. Paris, 640 pp.

DOBZHANSKY, THEODOSIUS.

1940. Speciation as a stage in evolutionary divergence. *Amer. Naturalist*, vol. 74, pp. 312-321.

- DORST, JEAN (translated by C. D. Sherman).
1962. The migrations of birds. 476 pp. Boston.
- DOUAUD, JOSEPH.
1957. Las migrations au Togo (Afrique occidentale). *Alauda*, vol. 25, pp. 241-266.
- DROST, RUDOLF.
1950. Study of bird migration 1938-1950. Proc. 10th Intern. Ornith. Congress, Uppsala, pp. 216-240.
- ELLENBERGER, P. M.
1951. Notes on some birds of the Ndanga (Zaka) District of Southern Rhodesia. *Ostrich*, vol. 22, pp. 17-24.
- ERGENE, SAADET.
1945. *Türkiye Kuslari*. Istanbul, 361 pp., 104 pls.
- ERLANGER, CARLO FREIHERR VON.
1900. Beiträge zur Avifauna Tunisiens. *Journ. f. Ornith.*, vol. 48, pp. 1-105.
1905. Beiträge zur Vogelfauna Nordostafrikas, pt. III. *Journ. f. Ornith.*, vol. 53, pp. 433-499.
- ETCHÉCOPAR, R. D.
1942. Polymorphisme des oeufs d'oiseux. *L'Oiseau et Rev. Française d'Ornith.*, n.s., vol. 12, pp. 121-132.
1946. Considerations sur le dernier ouvrage de Stuart Baker: "Cuckoo Problems." *L'Oiseau et Rev. Française d'Ornith.*, n.s., vol. 16, pp. 153-167.
- FELL, H. BARRACLOUGH.
1947. The migration of the New Zealand bronze cuckoo, *Chalcites lucidus lucidus* (Gmelin). *Trans. Royal Soc. New Zealand*, vol. 76, pp. 504-515.
- FINSCH, OTTOW, and HARTLAUB, CARL JOHANN GUSTAVE.
1870. Die Vögel Ost-Afrikas. In Baron Carl Claus von der Decken's Reisen in Ost Afrika in 1859-61, vol. 4, viii + 897 pp., 11 pls. Leipzig.
- FISCHER, G. A.
1885. Uebersicht der in Ostafrika gesammelten Vogelarten, mit Angabe der verschiedenen Fundorte. *Journ. f. Ornith.* vol. 33, pp. 113-142.
- FISCHER, G. A., and REICHENOW, A.
1878. Uebersicht der von Dr. G. A. Fischer auf Sansibar und während einer Reise durch das Küstenland von Mombassa bis Wito gesammelten oder sicher beobachteten Vögel. *Journ. f. Ornith.*, vol. 26, pp. 247-268.
- FORBES, W. A.
1885. The collected scientific papers of the late William Alexander Forbes. London, xv + 496 pp., 25 pls.
- FORD, E. B.
1945. Polymorphism. *Biol. Review*, vol. 20, pp. 73-88.
- FRADE, F.
1951 (=1953). Catalogo das Aves de Mocambique. *Anais Junta de Investigações Coloniais*, vol. 6, tomo 4, fasc. 4. *Estudios de Zoologia*, pp. 7-294.
- FRASER, W.
1962. Colour of cuckoo eggs. *African Wild Life*, vol. 16, No. 4, p. 343.

FRIEDMANN, HERBERT.

1929. The cowbirds. A study in the biology of social parasitism. Springfield, Ill., 421 pp., 28 pls., 12 text figs.
1930. Birds collected by the Childs Frick expedition to Ethiopia and Kenya Colony. Part I, Non-Passerres. U.S. Nat. Mus., Bull. 153, 516 pp.
- 1949a. The parasitic cuckoos of Africa. Washington Acad. Sci., Monograph No. 1 (1948), xii + 204 pp., 10 pls.
- 1949b. Additional data on African parasitic cuckoos. Ibis, vol. 91, pp. 514-519.
1956. Further data on African parasitic cuckoos. Proc. U.S. Nat. Mus., vol. 106, pp. 377-408.
1960. The parasitic weaverbirds. U.S. Nat. Mus., Bull. 223, 196 pp.

FRIEDMANN, HERBERT, and LOVERIDGE, ARTHUR.

1937. Notes on the ornithology of tropical East Africa. Bull. Mus. Comp. Zool., vol. 81, pp. 1-413.

FÜRBRINGER, MAX.

1888. Untersuchungen zur Morphologie und Systematik der Vögel . . . 2 vols. Amsterdam.

GILBERT, ANT.

1925. L'Oxylophie geai en Camargue. Rev. Française d'Ornith., vol. 9, année 17, No. 190, pp. 59-60.

GILL, E. H. N.

1925. A description of the nests and eggs of the common birds occurring in the plains of the United Provinces. Journ. Bombay Nat. Hist. Soc., vol. 30, pp. 273-284.

GILLET, H.

1960. Observations sur l'Avifaune du Massif de L'Ennedi (Tchad). L'Oiseau et la Rev. Française d'Ornith., vol. 30, No. 2, pp. 99-134.

GLADKOV, N.

1960. Systema Avium Rossicarum Ordo Cuculi ou Cuculiformes. L'Oiseau et Rev. Française d'Ornith., vol. 30, special supplement, pp. 215-217.

GODFREY, ROBERT.

1934. Notes on cuckoos from eastern Cape Province. Oolog. Rec., vol. 14, pp. 67-69.
1939. The black-crested cuckoo. Ostrich, vol. 10, pp. 21-27.

GRANT, CLAUDE HENRY BAXTER.

1915. On a collection of birds from British East Africa and Uganda presented to the British Museum by Capt. G. P. Cosenss. Ibis, ser. 10, vol. 3, pp. 400-473.

GRANT, CLAUDE HENRY BAXTER, and MACKWORTH-PRAED, CYRIL WINTHROP.

1936. Notes: 1. On *Cuculus clamosus* Latham and *Cuculus jacksoni* Sharpe.
2. On the status of *Coccystes albonotatus* Shelley and *Coccystes caroli* Norman. Bull. Brit. Ornith. Club, vol. 56, pp. 123-126.
1948. On the movements in the non-breeding season of *Clamator jacobinus serratus* (Sparrman). Bull. Brit. Ornith. Club, vol. 68, pp. 171-172.

GRANVIK, HUGO.

1923. Contributions to the knowledge of East African ornithology. Journ. f. Ornith., vol. 71, suppl., 280 pp., 11 pls.

1934. The ornithology of northwestern Kenya Colony with special regard to the Suk and Turkana District. *Rev. Zool. Bot. Africaines*, vol. 25, fasc. 1, pp. 1-190, 4 pls.
- GRAY, W. J.
1945. Some notes on the nesting of certain birds in northern Nyasaland. *Ostrich*, vol. 16, pp. 49-54.
- GROTE, HERMANN.
1936. Neue Beiträge zur Kenntnis der palaearktischen Zugvögel in Afrika. *Mitt. Mus. Berlin*, vol. 22, pp. 45-85.
- GYLDENSTOLPE, NILS.
1921. Zoological results of the Swedish expedition to central Africa 1921. *Vertebrata* 1, Birds. *Kungl. Svenska Vetenskaps. Handl.*, ser. 3, vol. 1, No. 3, 326 pp., 2 pls.
- HAAGNER, ALWIN KARL.
1905. A further contribution to the ornithology of Modderfontein, Transvaal. *Journ. S. Afr. Ornith. Union*, vol. 1, pp. 48-56.
- HAAGNER, ALWIN KARL, and IVY, ROBERT H.
1907a. The birds of Albany Division, Cape Colony. *Journ. S. Afr. Ornith. Union*, vol. 3, pp. 76-116.
1907b. Sketches of South African bird-life. Cape Town, 316 pp., 158 figs.
- HAARTMAN, LARS VON.
1957. Adaptation in hole-nesting birds. *Evolution*, vol. XI, pp. 339-347.
- HALDANE, J. B. S.
1932. The causes of evolution. London, 235 pp.
- HARDY, A. C.
1954. Escape from specialization. *In* *Evolution as a process*. Ed. by J. S. Huxley, A. C. Hardy, and E. B. Ford. Pp. 122-142.
- HARDY, E.
1940. Bird migration. *Quart. Rev.*, London, vol. 274, pp. 219-232.
- HARRISON, C. J. O.
1963. Eggshell pigmentation in the Jacobin cuckoo, *Clamator jacobinus* (Bodd.). *Bull. Brit. Ornith. Club*, vol. 83, pp. 154-155.
- HARTERT, ERNST.
1912. Die Vögel der palaearktischen Fauna, vol. 2. Berlin, pp. xxiv + 833-1764.
1915. List of a small collection of birds from Hausaland, Northern Nigeria. *Novitates Zool.*, vol. 22, pp. 244-266.
1927. Die Brutzeiten der Vögel in Klein-Afrika (final part). *Beitr. z. Fortpflanzungsbiol. d. Vögel*, vol. 3, pp. 188-204.
- HARTERT, ERNST, and JOURDAIN, FRANCIS CHARLES ROBERT.
1923. The hitherto known birds of Morocco. *Novitates Zoologicae*, vol. 30, pp. 91-152.
- HARTLAUB, GUSTAV.
1881. Beitrag zur Ornithologie der östlich-äquatorialen Gebiete Afrika's. Nach Sendungen und Noten von Dr. Emin Bey in Lado. *Abhandl. Naturwiss. Ver. Bremen*, vol. 7, pp. 83-128.
- HAVERSCHMIDT, FRANÇOIS.
1961. Der Kuckuck *Tapera naevia* und seine Wirte in Surinam. *Journ. f. Ornith.*, vol. 102, pp. 353-359.

HEINRICH, GERD.

1958. Zur Verbreitung und Lebensweise der Vögel von Angola. Journ. f. Ornith., vol. 99, pp. 322-362.

HEINROTH, OSKAR.

1922. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht und Brutdauer. Journ. f. Ornith., vol. 70, pp. 172-285.

HEUGLIN, MARTIN THEODOR VON.

- 1869-1873. Ornithologie Nordost-Afrika's der Nilquellen und Küstengebiete des Rothen Meeres und des nördlichen Somal-Landes. 2 vols., cccxxv + 1512 pp., 51 pls.

(HEWITT, JOHN).

1931. A guide to the vertebrate fauna of the eastern Cape Province. Pt. 1. Mammals and Birds. 256 pp.

HOESCH, WALTER.

1934. *Lamprocolius nitens bispecularis* als Wirtsvogel von *Clamator glandarius*. Ornith. Monatsb., vol. 42, pp. 68-70.

1939. Kritische Betrachtungen zum Problem des Brutparasitismus bei den afrikanischen Viduinen. Beiträg. zur Fortpflanzungsbiol. der Vögel, vol. 15, pp. 200-214.

1955. Der Vogelwelt südwestafrikas. Windhoek, 300 pp.

HOESCH, WALTER, and NIETHAMMER, G.

1940. Die Vogelwelt Deutsch-Südwestafrikas. Journ. f. Ornith., vol. 88, Sonderheft, 404 pp., 1 pl., 76 figs.

HOPWOOD, CYRIL.

1912. A list of birds from Arakan. Journ. Bombay Nat. Hist. Soc., vol. 21, pp. 1196-1221.

HUE, F.

1945. Nouveaux cas de nidification du Coucou-Geai, *Clamator glandarius* en France. Oiseau, vol. 15, pp. 89-93.

1952. Nouvelles observations sur le Coucou Geai en France. Oiseau, vol. 22, pp. 303-316.

1953. Note sur le Coucou-geai dans le Midi de la France. Oiseau, n.s., vol. 23, pp. 297-299.

HUME, A. O., and OATES, E. W.

1890. The nests and eggs of Indian birds. Vol. 2, 420 pp. London.

HUXLEY, JULIAN S.

1927. On the relation between egg-weight and body-weight in birds. Journ. Linn. Soc. London, Zool., vol. 36, pp. 457-466.

1955. Morphism and evolution. Heredity, vol. 9, pp. 1-52.

IRBY, LT. COL. L. HOWARD.

1875. The ornithology of the Straits of Gibraltar. London, 236 pp.

IVY, R. H.

1901. Notes on the nesting and other habits of some South African birds. Ibis, ser. 8, vol. 1, pp. 18-28.

JACKSON, FREDERICK JOHN (completed by W. L. Sclater).

1938. The birds of Kenya Colony and the Uganda Protectorate. 3 vols., 1592 pp., 24 pls., 241 text figs. London.

JAMES, H. W.

1925. Birds observed in the Somerset East District, Cape Province, Union of South Africa. Ibis, ser. 12, vol. 1, pp. 621-648.

JEROME, C. H.

1943. Difficulties of amateur ornithologists in identifying the eggs of parasitic birds. *Ostrich*, vol. 14, pp. 99-103.

JONES, HUMPHREY.

1945. Notes on some birds of the Northern Rhodesia copperbelt. *Ostrich*, vol. 16, pp. 176-183.

JOURDAIN, FRANCIS CHARLES ROBERT.

1910. Exhibition of eggs from Cyprus. *Bull. Brit. Ornith. Club*, vol. 27, p. 27.

1920. Exhibition of a clutch of eggs of the kestrel with an egg of the great spotted cuckoo. *Bull. Brit. Ornith. Club*, vol. 40, p. 72.

1925. A study on parasitism in the cuckoos. *Proc. Zool. Soc. London*, pp. 639-667.

1936. The birds of southern Spain. *Ibis*, ser. 13, vol. 6, pp. 725-763.

JOURDAIN, FRANCIS CHARLES ROBERT, and SHUEL, RONALD.

1935. Notes on a collection of eggs and breeding habits of birds near Lokoja, Nigeria. *Ibis*, ser. 13, vol. 5, pp. 623-663.

JOVETIC, R.

1955. Apparition du Coucou-geai (*Clamator glandarius* [L.]) en R. P. De Macedoine (Yougoslavie). *L'Oiseau*, n.s., vol. 25, pp. 206-210.

JUBB, R. A.

1952. Some notes on birds of Southern Rhodesia. *Ostrich*, vol. 23, pp. 162-164.

KEAY, R. W.

1959. Oxford vegetation map of Africa south of the Tropic of Cancer. 24 pp. of text, 1 map.

KINNEAR, NORMAN B.

1922. On the birds collected by Mr. A. F. R. Wollaston during the first Mt. Everest expedition. *Ibis*, ser. 11, vol. 4, pp. 495-526.

KINNEAR, NORMAN B., and WHISTLER, HUGH.

1930. The Vernay scientific survey of the eastern Ghats. *Ornithological Section, Journ. Bombay Nat. Hist. Soc.*, vol. 34, No. 2, pp. 386-403.

KOENIG, ALEXANDER.

1920. Die Sitzfüssler (Insessores) Aegyptens. *Journ. f. Ornith.*, vol. 68, Sonderheft, 148 pp.

- 1931 (n.d.). Katalog der Nido-Oologischen Sammlung im Museum Alexander Koenig. Band I. 352 pp.

KRÜPER, TH.

1875. Beitrag zur Ornithologie Klein-Asiens. *Journ. f. Ornith.*, vol. 23, pp. 258-285.

KUMMERLÖWE, HANS, and NIETHAMMER, GÜNTHER.

1935. Beiträge zur Kenntnis der Avifauna Kleinasiens (Paphagonien-Galatien). *Journ. f. Ornith.*, vol. 83, pp. 25-75.

KUTTER, DR.

1878. Betrachtungen über systematic und Oologie vom Standpunkte der Selectionstheorie. *Journ. f. Ornith.*, vol. 26, pp. 300-348.

LACK, DAVID LAMBERT.

1942. Ecological features of the bird fauna of British small islands. *Journ. Animal Ecol.*, vol. 11, pp. 9-36.

- 1943-44. The problem of partial migration. *Brit. Birds*, vol. 37, pp. 122-130, 143-150.
- 1947a. The significance of clutch size. *Ibis*, vol. 89, pp. 302-335.
- 1947b. Darwin's finches. Cambridge University Press, 208 pp., 9 pls., 27 figs.
1951. Population ecology in birds. A review. *Proc. 10th Int. Ornith. Congress*, 1950, Uppsala, pp. 409-448.
1954. The natural regulation of animal numbers. Oxford, 343 pp.
- LAFERRERE, MARC.
1956. L'Oxylope *Clamator glandarius* (Lin.) dans les pinèdes de l'Esterel et de la cote Varoise. *Alauda*, vol. 24, pp. 275-286.
- LAMBRECHT, KALMAN.
1933. *Handbuch der Palaeornithologie*. 1022 pp., 4 pls., 209 text figs.
- LAMM, DONALD W.
1955. Local migratory movements in Southern Mozambique. *Ostrich*, vol. 26, pp. 32-37.
- LAYARD, EDGAR LEOPOLD.
- 1875-84. The birds of South Africa, new ed. London, 890 pp., 12 pls.
1877. Note on two African cuckoos of the genus *Coccytes*. *Proc. Zool. Soc. London*, pp. 465-466.
- LEIGH, M. G.
1942. Notes on the jacobin cuckoo. *Ostrich*, vol. 13, pp. 105-107.
- LEVAILLANT, FR.
1806. *Histoire Naturelle des Oiseaux d'Afrique*. Vol. 5, pp. 160. Paris.
- LEVEQUE, R.
1957. Notes sur la distribution et l'extension du Coucou-geai en France méditerranéenne. *Alauda*, vol. 25, pp. 227-229.
- LILFORD, LORD.
1866. Notes on the ornithology of Spain. *Ibis*, No. 5, vol. 2, pp. 173-187.
- LINCOLN, FREDERICK CHARLES.
1939. The individual *vs.* the species in migration studies. *Auk*, vol. 56, pp. 250-254.
- LINSDALE, JEAN MYRON.
1937. The natural history of magpies. *Pacific Coast Avifauna*, No. 25, 234 pp.
- LIVERSIDGE, R.
1961. Pre-incubation development of *Clamator jacobinus*. *Ibis*, vol. 103a, p. 624.
- LIVESEY, T. R.
1935. Cuckoo problems. *Journ. Bombay Nat. Hist. Soc.*, vol. 38, pp. 734-758.
- LÖNNBERG, EINAR.
1929. The development and distribution of the African fauna in connection with and depending upon climatic changes. *Ark. Zool.*, vol. 21 A, No. 4, pp. 1-33, 5 figs.
- LOVERIDGE, ARTHUR.
1922. Notes on East African birds (chiefly nesting habits and stomach contents) collected 1915-1919. *Proc. Zool. Soc. London*, pp. 837-862.

LOWE, WILLOUGHBY P.

1921. The birds of Tasso and adjoining islands of the Rockelle River, Sierra Leone. *Ibis*, ser. 11, vol. 3, pp. 265-282.
1937. Report on the Lowe-Waldron expedition to the Ashanti forests and Northern Territories of the Gold Coast. *Ibis*, ser. 14, vol. 1, pp. 635-662, 830-864.

LUCANUS, FREDRICH VON.

1921. Zur Frage der Mimikry der Kuckuckseier. *Journ. f. Ornith.*, vol. 69, pp. 239-258.

LYNES, HUBERT.

- 1924-25. On the birds of north and central Darfur, with notes on the west-central Kordofan and North Nuba Provinces of the British Sudan. *Ibis*, ser. 11, vol. 6, pp. 399-446, 648-719; ser. 12, vol. 1, pp. 71-131, 344-416, 541-590, 758-797.
1934. Birds of the Ubena-Uhehe highlands and Iringa uplands. *Journ. f. Ornith.*, vol. 82, suppl., 147 pp., 15 pls.
1938. Contribution to the ornithology of the southern Congo Basin. Lynes-Vincent tour of 1933-34. *Rev. Zool. Bot. Africaines*, vol. 31, pp. 1-128, pls. 1-13.

MACDONALD, MALCOLM.

1960. Birds in my Indian garden. London, 192 pp.

MACKWORTH-PRAED, CYRIL WINTHROP, and GRANT, CLAUDE HENRY BAXTER.

1937. Systematic notes on East African birds.—Part XIV. 32. On the relationship of *Clamator serratus* (Sparrm.) *Clamator jacobinus pica* (Hempr. and Ehr.), and *Clamator hypopinarus* (Cab. and Heine). *Ibis*, ser. 14, vol. 1, pp. 402-406.
1952. Birds of Eastern and North Eastern Africa, vol. 1, xxv + 836 pp., 59 pls. London, New York.

MADDEN, J. F.

1930. Bird migration in the Red Sea Province. *Sudan Notes and Records*, vol. 12, pp. 123-135.
1934. Notes on the birds of southern Darfur. *Sudan Notes and Records*, vol. 17, pp. 83-101.

MAKATSCH, WOLFGANG.

1951. Über den Brutparasitismus der Vögel. *Urania*, vol. 14, pp. 210-216.
1955. Der Brutparasitismus in der Vogelwelt. 236 pp.

MALBRANT, R.

1952. Faune du Centre Africain Français (mammifères et oiseaux), ed. 2. *In* Encyclopedie biologique, vol. 15, 616 pp., 32 pls., 129 figs. Paris.

MALBRANT, R., and MACLATCHY, A. R.

1949. La faune de l'Equateur Africain français. Tome 1, Oiseaux. 460 pp., 119 figs., 12 pls.

MALZY, P.

1962. La Faune Avienne du Mali. *L'Oiseau et Rev. Française d'Ornith.*, vol. 32, special number, pp. 1-81.

MARCHANT, S.

1953. Notes on the birds of south-eastern Nigeria. *Ibis*, vol. 95, pp. 38-69.
1963. The breeding of some Iraqi birds. *Ibis*, vol. 105, pp. 516-557.

MAYR, ERNST.

1957. Evolutionary aspects of host specificity among parasites of vertebrates. Premier Sympos. sur la specificite parasitaire des parasites de Vertebres. Union Internat. Sci. Biol., ser. B, vol. 32, pp. 7-18.
1959. Change of genetic environment and evolution. *In* Evolution as a process, ed. by J. S. Huxley, A. C. Hardy, and E. B. Ford. Pp. 157-180.

MAYR, ERNST, and MEISE, WILHELM.

1930. Theoretisches zur Geschichte des Vogelzugs. Vogelzug, vol. 1, pp. 149-172.

MCLACHLAN, G. R., and LIVERSIDGE, R.

1957. Roberts' birds of South Africa. Rev. ed. 504 pp., 56 pls. Cape Town.

MEIKLEJOHN, M. F. M.

1940. Notes on migratory birds from the southern shores of Lake Victoria. December 22, 1939, to February 28, 1940. Ostrich, vol. 11, pp. 33-40.

MEINERTZHAGEN, RICHARD.

1922. Notes on some birds from the Near East and from tropical East Africa. Ibis, ser. 11, vol. 4, pp. 1-74.
1930. Nicoll's birds of Egypt, vol. 1, 348 pp., 15 pls. London.
1948. The birds of Ushant, Brittany. Ibis, vol. 90, pp. 553-567.
1951. Some relationships between African, Oriental, and Palearctic genera and species, with a review of the genus Monticola. Ibis, vol. 93, pp. 443-459.
1954. The birds of Arabia. 624 pp., 18 pls. Edinburgh, London.

MEISE, WILHELM.

1930. Zum Problem der Brutschmarotzertums. Beitr. Fortpflanz Vögel, vol. 6, pp. 119-131.
1937. Zur Vogelwelt des Matengo-Hochlandes nahe dem Nordende des Njassasees. Mitt. Zool. Mus. Berlin, vol. 22, pp. 86-160, 4 pls.

MEYER, H. F.

1959. Great spotted cuckoo parasitizing a hole-nesting species in Southern Rhodesia. Ostrich, vol. 30, p. 85.

MILSTEIN, PETER.

1954. An egg problem. Bokmakerie, vol. 6, pp. 4-5.

MOLTONI, EDGARDO.

1940. Gli Uccelli dell Africa Orientale Italiana. Parta Prima. Milano, 261 pp., 38 pls.

MOORE, H. J. and BOSWELL, C.

1956. Field observations on the birds of Iraq. Pt. II. Publ. No. 10, Iraq Nat. Hist. Mus., pp. 111-213.

MOREAU, REGINALD ERNEST.

- 1937-38. Amami Memoirs. The avifauna of the mountains along the Rift Valley in north central Tanganyika Territory (Mbulu Distr.). Pts. 1 & 2. Ibis, ser. 14, vol. 1, pp. 760-768; vol. 2, pp. 1-32.
1937. Migrant birds in Tanganyika Territory. Tanganyika Notes and Records, No. 4, pp. 17-50.
1938. Bird migration over the north western part of the Indian Ocean, the Red Sea, and the Mediterranean. Proc. Zool. Soc. London, vol. 108A, pp. 1-26.

1949. Special Review. Friedmann on African cuckoos. *Ibis*, vol. 91, pp. 529-537.
1951. The migration system in perspective. *Proc. 10th Internat. Ornith. Congress*, 1950, pp. 245-248.
1952. The place of Africa in the Palearctic migration system. *Journ. Anim. Ecol.* vol. 21, pp. 250-271.
1954. The main vicissitudes of the European avifauna since the Pliocene. *Ibis*, vol. 96, pp. 411-431.
- MORGAN, A. G.
1956. The redwing. *Journ. St. Andrews College Nat. Hist. Soc., Grahams-town, Cape Province*, vol. 3, No. 1, p. 15.
- MORGAN, RHODES W.
1875. On the nidification of certain south-Indian birds. *Ibis*, ser. 3, vol. 5, pp. 313-323.
- MOUNTFORT, GUY.
1958. *Wild paradise*. Boston, 240 pp., 59 pls.
- MOUNTFORT, GUY, and FERGUSON-LEES, I. J.
1961. The birds of the Coto Doñana. *Ibis*, vol. 103a, pp. 86-109.
- MÜLLER, AUGUST.
1879. Zur Ornithologie der Insel Cypern. *Journ. f. Ornith.*, vol. 27, pp. 385-393.
- MUSSELWHITE, D. W.
1923. Oviposition of cuckoo in domed nests. *Bull. Brit. Ornith. Club*, vol. 44, pp. 30-32.
- NEHRKORN, A.
1899. *Katalog der Eiersammlung*. Braunschweig, 256 pp., 4 pls.
- NEUMANN, OSCAR.
1900. Beiträge zur Vogelfauna von Ost- und Central-Africa. Pt. III. *Journ. f. Ornith.*, vol. 48, pp. 185-228.
1904. Vögel von Schoa und Süd-Äthiopien. Ploceidae. *Journ. f. Ornith.*, vol. 52, pp. 321-410.
- NICE, MARGARET MORSE.
1937. Studies on the life history of the song sparrow. Pt. I. *Trans. Linnaean Soc. New York*, vol. 4, pp. 1-247.
- NICOLAI, J.
1961. Die Stimmen einiger Viduinen. *Journ. f. Ornith.*, vol. 102, pp. 213-214.
- NIETHAMMER, G.
1955. Zur Systematik der Vögel des Kaoko-Veldes (Südwestafrika). *Bonner Zool. Beiträge*, vol. 6, pp. 173-195.
- NOBLE, HEATLEY.
1902. Forty-four days' nesting in Andalucia. *Ibis*, ser. 8, vol. 2, pp. 67-89.
- NORMAN, GEORGE CAMERON.
1888. Note on the geographical distribution of the crested cuckoos (*Coccyzus*). *Ibis*, ser. 5, vol. 6, pp. 396-409.
- OATES, EUGENE W., and REID, SAVILLE G.
1903. *Catalogue of birds' eggs in the British Museum*. Vol. 3, 349 pp., 10 pls. London.
- OGILVIE-GRANT, WILLIAM ROBERT.
1912. *Catalogue of birds' eggs in the British Museum*. Vol. 5, 457 pp., 22 pls. London.

OSMASTON, B. B.

1916. Notes on cuckoos in Maymyo. Journ. Bombay Nat. Hist. Soc., vol. 24, pp. 359-363.

1927. Notes on the birds of Kashmir. Pt. II. Journ. Bombay Nat. Hist. Soc., vol. 32, pp. 134-153.

PAKENHAM, R. H. W.

1948. Field notes on the birds of Zanzibar and Pemba Islands. 5th ser. Ibis, vol. 90, pp. 98-102.

PALUDAN, KNUD.

1936. Report on the birds collected during Professor O. Olufsen's expedition to French Sudan and Nigeria in the year 1927; with field-notes by the collector, Mr. Harry Madsen. Vidensk-Medd. fr. Dansk naturh. Foren, vol. 100, pp. 247-346.

1938. Zur Ornithologie des Zagros-Gebietes, W. Iran. Journ. f. Ornith., vol. 86, pp. 562-638.

PETERS, JAMES LEE.

1940. Check-list of birds of the world. Vol. 4, 291 pp. Cambridge.

PHILLIPS, W. W. A.

1948. Cuckoo problems in Ceylon. Spolia Zeylanica, vol. 25, pt. 2, pp. 45-60.

PIKE, E.

1954. The birds of Blythwood and some notes on birds of the district. Ostrich, vol. 25, pp. 115-129.

PINTO, A. ROSA.

1953. Uma lista sistemática das Aves de região extremo sul da Província de Moçambique. Bol. Soc. Est. Moçambique, No. 77, pp. 1-27.

PITMAN, CHARLES ROBERT S.

1931. Variation in the plumage of Lavaillant's cuckoo, *Clamator cafer* (Licht.). Bateleur, vol. 3, p. 50.

1962. Comments on some breeding records in "The Birds of British Somaliland and the Gulf of Aden" in vol. III by Sir Geoffrey Archer and Eva M. Godman. Pt. 1. Oologists' Record, vol. 36, pp. 22-27.

1963a. Comments on some breeding records in "The Birds of British Somaliland and the Gulf of Aden," vol. IV, by Sir Geoffrey Archer and Eva M. Goodman. Oologists' Record, vol. 37, pp. 49-54.

1963b. The breeding of the great spotted cuckoo, *Clamator glandarius* L., in Iraq, and a note on the Iraq eggs of the Kashmir magpie, *Pica pica bactriana* Bp. Bull. Brit. Ornith. Club, vol. 83, pp. 9-11.

PLOWES, DARRELL CHARLES HERBERT.

1946. Data of birds' eggs in my collection. Pt. 2. Ostrich, vol. 17, pp. 111-121.

1947. The birds of Ladysmith, Natal. Ostrich, vol. 18, pp. 134-154.

PLOWES, DARRELL C. H., and CUSACK, E.

1944. A brief survey of the birds of Bloemhof district. Ostrich, vol. 15, pp. 81-103.

PONCE DE LEON, PEDRO DIEZ, and DEETJEN, HANS.

1956. Über die Vogelwelt der Umgebung von Madrid. Ornith. Mitteilungen, vol. 8, pp. 124-126.

POULTON, E. B.

1926. The evolution of the colours and patterns of cuckoos' eggs and its relation to that of insect resemblances such as mimicry. Proc. Ent. Soc. London (for 1925), pp. xcii-xciv.

PRIEST, CECIL DAMER.

1934. The birds of Southern Rhodesia, vol. 2, 553 pp., 10 pls., 172 figs. London and Beccles.

1948. Eggs of birds breeding in Southern Africa. Glasgow, 180 pp., 20 pls.

PRINGLE, V. L.

1948. Egg records of cuckoos. Ostrich, vol. 19, pp. 155-156.

PROCTER, F. W.

1909. Exhibition of eggs. Bull. Brit. Ornith. Club, vol. 23, pp. 59-60.

RAND, AUSTIN LOOMER, FRIEDMANN, HERBERT, and TRAYLOR, MELVIN A.

1959. Birds from Gabon and Moyen Congo. Fieldiana, Zool., vol. 41, no. 2, pp. 223-411.

RAW, W.

1921. Field notes on the birds of Lower Egypt. With contributions by Col. R. Sparrow and the Rev. F. C. R. Jourdain. Ibis, ser. 3, vol. 3, pp. 359-387.

REICHENOW, ANTON.

1897. Über die Pflegeeltern von *Coccyzus serratus*. Ornith. Monatsb., vol. 5, p. 112.

1902-03. Die Vogel Afrikas, vol. 2. 752 pp.

REID, S. G.

1885. Winter notes from Morocco. Ibis, ser. 5, vol. 3, pp. 241-255.

REISER, O.

1913. Ueber die Erbeutung eines Häherkuckucke, *Clamator glandarius* (L.) und eine wichtige Oertlichkeit zur Beobachtung des Vogelzuges. Ornith. Jahrb., vol. 24, pp. 81-85.

RENNIE, FERGUS.

1944. Letter to editor. Ostrich, vol. 15, p. 144.

RENSCH, BERNARD.

1924. Zur Entstehung der Mimikry der Kuckuckseier. Journ. f. Ornith., vol. 72, No. 4, pp. 461-472.

1925. Das Problem des Brutparasitismus bei Vögeln. Sitzungsber. Ges. Naturf. Freunde, Berlin, pp. 55-69.

REY, EUGENE.

1871. Jugendkleider und Eier einiger Vögel aus Klein Asien. Journ. f. Ornith., vol. 19, pp. 459-462.

1872. Zur Fortpflanzungsgeschichte unseres Kukuks. Zool. Garten, pp. 241-243.

1872. Zur Ornith. von Portugal. Journ. f. Ornith., vol. 20, pp. 140-155.

1892. Altes und neues aus dem Haushalte des Kuckucks. Leipzig. 108 pp.

RHODESIAN ORNITHOLOGICAL SOCIETY.

1959. Report on nest record cards. Bokmakeirie, vol. 11, pp. 19-20.

RIPLEY, S. DILLON.

1961. A synopsis of the birds of India and Pakistan; together with those of Nepal, Sikkim, Bhutan, and Ceylon. xxxvi + 702 pp., 2 double maps (one colored) with overlays. The Bombay Natural History Society, Madras.

ROBERTS, AUSTIN.

1924. Synoptic check list of the birds of South Africa. Annals Transvaal Mus., vol. 10, pp. 89-195, pls. 2-5.

1932. Migration of African birds. Ostrich, vol. 3, pp. 97-109.
1938. Reviews and records. Ostrich, vol. 9, pp. 105-119.
- 1939a. Notes on the eggs of parasitic birds in South Africa. Ostrich, vol. 10, pp. 1-20, 100-117.
- 1939b. Swifts and other birds nesting in buildings. Ostrich, vol. 10, pp. 85-99.
1942. Review of Baker's "Cuckoo Problems." Ostrich, vol. 13, pp. 182-183.
- ROBERTS, AUSTIN (rev. by McLACHLAN, G. R., and LIVERSIDGE, R.).
1957. Birds of South Africa. Cape Town, 504 pp., 56 pls.
- ROBERTS, E. L.
1954. The birds of Malta. Malta, 168 pp.
- SAUNDERS, HOWARD.
1869. Notes on the ornithology of Italy and Spain. Ibis, ser. 2, vol. 5, pp. 391-403.
- SCHIERMANN, G.
1926. Beitrag zur Schädigung der Wirtsvögel durch *Cuculus canorus*. Beitr. z. Fortpflanzungsbiol. der Vögel, vol. 2, pp. 28-30.
- SCHLUTER, WILHELM
1859. Zweifel am Nichtbrüten des *Oxylophus glandarius*. Journ. f. Ornith., vol. 7, pp. 238-239.
- SCHMALHAUSEN, I. I.
1949. Factors of evolution. The theory of stabilizing selection. (Transl. by I. Dordick, ed. by T. Dobzhansky). Philadelphia, 327 pp.
- SCHÖNWETTER, M.
1928. Anmerkungen zum Nehr Korn—Katalog (final part). Beitr. z. Fortpflanzungsbiol. d. Vögel, vol. 4, pp. 129-136.
- SCHOUTEDEN, HENRI.
1954. Faune du Congo Belge et du Ruanda Urundi. III. Oiseaux non Passereaux, Tervuren, 434 pp.
- SCHWEINFURTH, GEORGE; RATZEL, FRIEDRICH; FELKIN, ROBERT W.; and HARTLAUB, GUSTAV.
1888. Emin Pasha in Central Africa, being a collection of his letters and journals. London, 547 pp., 2 pls., map.
- SCLATER, WILLIAM LUTLEY.
1903. The birds of South Africa, commenced by Arthur Stark. Vol. 3, 416 pp. London.
1906. The migration of birds in South Africa. Journ. S. Afr. Ornith. Union, vol. 2, pp. 14-21.
1924. Systema avium Aethiopicarum. Pt. 1, 304 pp. London.
- SCLATER, WILLIAM LUTLEY, and MACKWORTH-PRAED, CYRIL WINTHROP.
1919. A list of the birds of the Anglo-Egyptian Sudan, based on the collections of Mr. A. L. Butler, Mr. A. Chapman, and Capt. H. Lynes, R. N., and Major Cuthbert Christy. Pt. III. Ibis, ser. 11, vol. 1, pp. 628-707.
- SERLE, WILLIAM.
1939. Field observations on some Northern Nigerian birds. Pt. I. Ibis, ser. 14, vol. 3, pp. 654-699.
1940. Field observations on some Northern Nigerian birds. Pt. II. Ibis, ser. 14, vol. 4, pp. 1-47.

1943. Further field observations on Northern Nigerian birds (cont.). *Ibis*, vol. 85, pp. 264-300.
1948. The birds of Sierra Leone, pt. 2. *Ostrich*, vol. 19, p. 187-199.
1957. A contribution to the ornithology of the eastern region of Nigeria. Pt. I. *Ibis*, vol. 99, pp. 371-418.
- SCHARPE, RICHARD BOWDLER.
1872. On recent collections of birds from the Fantee County, in Western Africa. *Ibis*, ser. 3, vol. 2, p. 66-74.
1873. On the Cuculidae of the Ethiopian region. *Proc. Zool. Soc. London*, pp. 578-624.
- SHELLEY, GEORGE ERNEST.
1881. List of birds recently collected by Dr. Kirk in Eastern Africa. *Proc. Zool. Soc. London*, pp. 561-602.
1885. On Mr. E. Lort Phillips's collection of birds from Somali-Land. *Ibis*, ser. 5, vol. 3, pp. 389-418.
1891. Catalogue of birds in the British Museum. Vol. 19: Indicatoridae, Capitonidae, Cuculidae, and Musophagidae, pp. 209-456.
- SHUFELDT, R. W.
1901. The osteology of the cuckoos (*Coccyges*). *Proc. Amer. Philos. Soc.*, vol. 40, pp. 4-51, pls. 1-2.
- SIBLEY, CHARLES G.
1960. The electrophoretic patterns of avian egg-white proteins as taxonomic characters. *Ibis*, vol. 102, pp. 215-284.
- SIMMONS, R. M.
1930. Migration of the pied crested-cuckoo (*Coccyzus jacobinus*). *Journ. Bombay Nat. Hist. Soc.*, vol. 34, pp. 252-253.
- SJÖSTEDT, Y.
1910. Wissenschaftliche Ergebnisse der schwedischen zoologischen Expedition nach Kilimandjaro, dem Meru und dem umgebenden Masaissteppen Deutsch-Ostafrikas, 1905-06; vol. 1, Vögel, 173 pp.
- SKEAD, C. J.
- 1951a. Cuckoo studies on a South African farm. *Ostrich*, vol. 22, pp. 163-175.
- 1951b. Recent records of interest. *Ostrich*, vol. 22, p. 197.
1955. Jacobin crested cuckoo parasitizing paradise flycatcher's nest. *Ostrich*, vol. 26, p. 46.
1962. Jacobin crested cuckoo, *Clamator jacobinus* (Boddaert), parasitizing the fork-tailed drongo, *Dicrurus adsimilis* (Bechstein). *Ostrich*, vol. 32, pp. 72-73.
- SMITH, K. D.
1951. On the birds of Eritrea. *Ibis*, vol. 93, pp. 201-233.
1957. An annotated check list of the birds of Eritrea. *Ibis*, vol. 99, pp. 307-337.
- SMITHERS, REAY H. N., IRWIN, M. P. STUART, and PETERSON, MARY L.
1957. A check list of the birds of Southern Rhodesia. Cambridge University Press, 175 pp.
- SMYTHIES, BERTRAM E.
1953. The birds of Burma. 2d ed. London and Edinburgh. 668 pp., 30 pls.
1960. The birds of Borneo. London and Edinburgh. 561 pp., 45 pls.

SOUTHERN, H. N.

1954. Mimicry in cuckoos' eggs. *In* Evolution as a process, ed. by J. S. Huxley, A. C. Hardy, and E. B. Ford. Pp. 219-232.

SPENCE, J. M.

1957. Notes on the black crested cuckoo, *Clamator jacobinus serratus*. Ostrich, vol. 28, p. 126.

STADLER, HANS.

1954. La voix du Coucou-geai, Parc d'Aranjuez 6. VI. 29. Alauda, vol. 19, pp. 178-180.

STRESEMANN, ERWIN.

1924. Mutationsstudien VIII. *Clamator serratus* (Sparrman). Journ. f. Ornith., vol. 72, pp. 79-83.
1926. Uebersicht über die . . . Mutationsstudien I-XXIV under ihre wichtigsten Ergebnisse. Journ. f. Ornith., vol. 74, pp. 377-385.
1928. Aves-Vögel. *In* Kuckenthal und Krumbach, Handbuch der Zoologie (1927-34), vol. 7, 899 pp., 944 figs. Berlin and Leipzig.
1947. *Laniarius nigerrimus* (Rchw.): a mutation of *Laniarius ferrugineus sublacteus* (Cassin). Ibis, vol. 89, pp. 518-519.

STRESEMANN, VESTA, and STRESEMANN, ERWIN.

1961. Die Handschwingen—Mauser der Kuckucke (Cuculidae). Journ. f. Ornith., vol. 102, pp. 317-352.

STRICKLAND, H. E.

1850. List of birds procured in Kordofan by Mr. J. Petherick. Proc. Zool. Soc. London, pt. 18, pp. 214-221.

SWYNNERTON, CHARLES FRANCIS MASSY.

1908. Further notes on the birds of Gazaland. Ibis, ser. 9, vol. 2, pp. 391-443.
1918. Rejection by birds of eggs unlike their own; with remarks on some of the cuckoo problems. Ibis, ser. 10, vol. 6, pp. 127-154.

SYMONDS, EDMOND.

1906. Notes on some migratory visitants to Kroonstad, Orange River Colony. Journ. S. Afr. Ornith. Union, vol. 2, pp. 24-26.

SYMONS, GODFREY.

1962. Indian mynah host to cuckoo. African Wild Life, vol. 16, p. 343.

SZIELASKO, A.

1913. Die Bedeutung der Eischalenstruktur der Vögel für die Systematik. Journ. f. Ornith., vol. 61, pp. 229-261.

TAYLOR, J. SNEYD.

1945. Notes on the birds of the Van Ryneveld's Pass Irrigation Lake, Graaff-Reineet. Ostrich, vol. 16, pp. 44-54.

TAYLOR, LIONEL E.

1906. The birds of Irene, near Pretoria, Transvaal. Journ. S. Afr. Ornith. Union, vol. 2, pp. 55-83.

THEMIDO, ANTONIO ARMANDO.

1952. Aves de Portugal. Memórias e estudos de Museo Zoologico da Universidade de Coimbra, No. 213, 241 pp.

THODAY, J. M.

1953. Components of Fitness. *In* Symposia of the Soc. Exp. Biol. VII. Evolution, pp. 96-113.

THORPE, WILLIAM HOMAN.

1930. Biological races in insects and allied groups. *Biol. Reviews and Biological Proc. Cambridge Philosophical Soc.*, vol. 5, pp. 177-212.

TICEHURST, CLAUDE B.

- 1922-1923. The birds of Sind, pt. 3. *Ibis*, ser. 11, vol. 4, pp. 526-572; vol. 5, pp. 1-43.

TOMLINSON, D.

1962. Cuckoo eggs vary in colour. *African Wild Life*, vol. 16, p. 260.

TOWNSEND, F. S.

1921. Eggs of *Coccystes cafer*. *S. Afr. Journ. Nat. Hist.*, vol. 3, pp. 220-222.

TRISTRAM, H. B., in HEWITSON, WILLIAM C.

1859. Recent discoveries in European oology. *Ibis*, vol. 1, pp. 76-80.

1866. On the ornithology of Palestine. II. *Ibis*, ser. 2, vol. 2, pp. 280-292.

UNDERWOOD, GARTH.

1954. Categories of adaptation. *Evolution*, vol. 8, pp. 365-377.

VALVERDE, JOSE A.

1953. Notes sur le Coucou-geai en Castille. *L'Oiseau et Rev. Française d'Ornith.*, vol. 23, pp. 288-296.

VAN SOMEREN, VICTOR GURNET LOGAN.

1916. A list of birds collected in Uganda and British East Africa with notes on their nesting and other habits. II, *Ibis*, ser. 10, vol. 4, pp. 373-472.

1922. Notes on the birds of East Africa. *Novitates Zoologicae*, vol. 29, pp. 1-246, 7 pls.

1929. Notes on the birds of Jubaland and the Northern Frontier, Kenya. *Journ. E. Afr. and Uganda Nat. Hist. Soc.*, vol. 9, pp. 25-70.

1931. Catalogue of the European and Asiatic Migrants to Kenya and Uganda. *Journ. E. Afr. and Uganda Nat. Hist. Soc.*, spec. suppl. No. 4, 40 pp.

1932. Birds of Kenya and Uganda, being addenda and corrigenda to my previous paper in "Novitates Zoologicae" XXIX, 1922. *Novitates Zoologicae*, vol. 37, pp. 252-380, 4 pls.

1956. Days with birds, studies of the habits of some East African species. *Fieldiana, Zool.*, vol. 38, 502 pp.

VERHEYEN, RENE.

1953. Oiseaux. In *Exploration du Parc National de l'Upemba*. Mission G. F. De Witte, fasc. 19. Brussels, Institut des Parcs Nationaux du Congo Belge, 687 pp., 5 pls., 45 figs.

VINCENT, ALFRED WILLIAM.

- 1946-47-49. On the breeding habits of some African birds (cont.). *Ibis*, vol. 88, pp. 48-67; vol. 89, pp. 163-204; vol. 91, pp. 111-139.

VINCENT, JACK.

1934. The birds of northern Portuguese East Africa. Pts. 4-5. *Ibis*, ser. 13, vol. 4, pp. 495-527, 757-799.

VOOVS, KAREL H.

1959. The relationship of the European and Aethiopian avifaunas. *Proc. First Pan-African Ornith. Congress*, pp. 34-39.

1960. Atlas of European birds. 284 pp.

WADLEY, N. J. P.

1951. Notes on the birds of central Anatolia. *Ibis*, vol. 93, pp. 63-89.

WEIGOLD, HUGO.

1913. Ein Monat Ornithologie in den Wüsten und Kulturoasen Nordwest-mesopotamiens und Innersyriens. Journ. f. Ornith., vol. 61, pp. 1-40.

WHISTLER, HUGH.

1916. A note on some birds of the Gujranwala District, Punjab. Journ. Bombay Nat. Hist. Soc., vol. 24, pp. 689-710.
1928. The migration of the pied crested cuckoo (*Clamator jacobinus*). Journ. Bombay Nat. Hist. Soc., vol. 33, pp. 136-145.
1931. An open letter to the editors. Journ. Bombay Nat. Hist. Soc., vol. 35, pp. 189-195.
1935. Popular handbook of Indian birds. 513 pp., 20 pls.

WHISTLER, HUGH and KINNEAR, NORMAN B.

1934. The Vernay scientific survey of the eastern Ghats (ornith. sect.), pt. IX. Journ. Bombay Nat. Hist. Soc., vol. 37, pp. 515-528.

WHITE, CHARLES MATTHEW NEWTON, and WINTERBOTTOM, JOHN MIAL.

1949. A check list of the birds of Northern Rhodesia. Lusaka, 168 pp.

WICKHAM, P. F.

1930. Notes on the birds of the Upper Burma hills. Journ. Bombay Nat. Hist. Soc., vol. 34, pp. 46-63.

WINTERBOTTOM, JOHN MIAL.

1942. A contribution to the ornithology of Barotseland. Ibis, ser. 14, vol. 6, pp. 337-389.
1960. The zoo-geographical affinities of the avifauna of the western Cape Province. Ibis, vol. 102, pp. 383-393.
1962. Some manuscript notes of S. F. Townsend for the period 1878-1925. Ostrich, vol. 33, pp. 66-71.

WITHERBY, HARRY FORBES.

1928. On the birds of central Spain with some notes on those of south-east Spain. Ibis, ser. 12, vol. 4, pp. 587-663.

WITHERBY, HARRY FORBES; JOURDAIN, FRANCIS CHARLES ROBERT; TICEHURST, NORMAN F.; and TUCKER, BERNARD W.

- 1938-41. The handbook of British birds. London, 4 vols.

WOLFSON, ALBERT.

1942. Regulation of spring migration in juncos. Condor, vol. 44, pp. 237-263.

WOOD, JOHN.

1911. Notes from East London. Journ. S. Afr. Ornith. Union, vol. 7, p. 51.

WOODWARD, R. B., AND WOODWARD, J. D. S.

1899. Natal birds. Pietermaritzburg, 215 pp., 1 pl.

WOOLLEY, C. H. F.

1946. Jacobin and black-crested cuckoo. Ostrich, vol. 17, p. 370.

ZEDLITZ, OTTO GRAF VON.

1910. Meine ornithologische Ausbeute in Nordost-Afrika. Journ. f. Ornith., vol. 58, pp. 731-807.

- 1915-16. Das Süd-Somaliland als zoogeographisches Gebiet, III. Journ. f. Ornith., vol. 63, pp. 1-69; vol. 64, pp. 1-120.



SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NUMBER 5

SOME BEHAVIOR PATTERNS OF
PLATYRRHINE MONKEYS
I. THE NIGHT MONKEY
(AOTUS TRIVIRGATUS)

By

M. MOYNIHAN

Director, Canal Zone Biological Area
Smithsonian Institution



(PUBLICATION 4533)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 23, 1964

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 146, NUMBER 5

SOME BEHAVIOR PATTERNS OF
PLATYRRHINE MONKEYS
I. THE NIGHT MONKEY
(AOTUS TRIVIRGATUS)

By

M. MOYNIHAN

Director, Canal Zone Biological Area
Smithsonian Institution



(PUBLICATION 4533)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 23, 1964

PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

CONTENTS

	Page
Introduction	1
General Habitus, Locomotion, and Feeding.....	3
Ordinary Grooming and Cleaning Activities.....	6
Hostile Behavior	8
Overt Attack Behavior.....	9
Overt Alarm or Escape Behavior.....	12
Display Behavior	15
Swaying	16
Silent Arch Postures.....	18
Other Visual Patterns.....	20
Gruff Grunts	22
Resonant Grunts	25
Screams	31
Low Trills	32
Moans	36
Locomotor Notes—Gulps and Sneeze-grunts.....	38
Discussion	43
Social Sniffing	47
Sexual Behavior and Associated or Related Patterns.....	48
Hoots	49
Rubbing	52
Copulations, Allogrooming, and Associated Patterns.....	54
Examples	59
Behavior of Young Animals.....	63
Previous Descriptions of Night Monkey Behavior Patterns.....	78
Summary	80
Acknowledgments	82
Bibliography	82

ILLUSTRATIONS

TEXT FIGURES

1. Two typical semierect preleaping postures.....	5
2. Four head-down postures.....	15
3. Arch postures	19
4. A typical Gruff Grunt, uttered by an adult.....	23
5. A relatively short Scream, uttered by an adult.....	31
6. Two long Screams, uttered by an adult.....	32
7. A Low Trill, uttered by an adult.....	33
8. One Moan, followed immediately by one Low Trill, uttered by an adult	33
9. One Sneeze-grunt, followed immediately by one Low Trill, uttered by an adult	34

	Page
10. One Moan, uttered by an adult.....	37
11. Two Gulps, uttered by an adult.....	39
12. A single "twanging" noise heard while recording adults.....	42
13. Three Hoots, uttered by an adult female.....	50
14. Positions and postures sometimes assumed by mated individuals during Allogrooming	56
15. Four typical "pure" Squeaks, uttered by an immature.....	67
16. A single very loud Squeak, uttered by an immature.....	68
17. A "pure" Squeak, followed by a longer note more or less perfectly intermediate between a Squeak and a short Scream. Uttered by an immature	69
18. A series of four notes uttered by an immature.....	70
19. Two loud trilling patterns, intermediate between "pure" High Trills and Screams, but most similar to the former. Uttered by an im- mature	72
20. Two Hoots, uttered by an immature male.....	75
21. A single "Brrrrp" sound, uttered by an immature.....	76
22. An infant uttering Squeaks.....	77

SOME BEHAVIOR PATTERNS OF
PLATYRRHINE MONKEYS
I. THE NIGHT MONKEY
(*Aotus trivirgatus*)

BY M. MOYNIHAN
Director, Canal Zone Biological Area
Smithsonian Institution

THIS is the first in a series of papers on some behavior patterns of New World monkeys. The main emphasis of these papers will be comparative. Special attention will be paid to social signal patterns (including hostile and sexual signals) and other patterns that differ significantly in the various species. It is hoped that analyses of these patterns may throw some light on the evolution of the group as a whole.

INTRODUCTION

The Night Monkey (also called "Owl Monkey" or "Douroucoulí") is a rather small monkey of distinctive appearance.

Although individuals vary considerably in proportions, all adults have relatively small heads and more or less elongated bodies. Their limbs are of moderate length, the hind limbs being somewhat longer than the front. Their tails are long and heavily furred, and not at all prehensile. The back, most of the head, and the outer surfaces of the limbs may be gray, brown, or even reddish brown, while most of the underside of the body and the inner surfaces of the limbs are usually clear buff or caramel colored. The upper part of the tail generally is the same color as the back, and the terminal half or two-thirds is blackish. The face and forehead are marked with conspicuous black and white stripes and patches (see the accompanying figures for an indication of the color pattern of Panamanian Night Monkeys). The distinctive appearance of the face is enhanced by the very large eyes. In bright light, the pupils are greatly contracted and the orange or hazel irides are conspicuous. In very dim light, the pupils expand enormously and the eyes appear to be completely black.

Young Night Monkeys look more like marmosets in some ways. They have relatively larger heads and shorter bodies and tails than

adults; and their eyes are relatively *smaller*, in proportion to the rest of the head (see figure 22).

This account is based primarily upon studies of captive animals, checked (whenever possible) by observations of wild animals living under natural conditions.

Fifteen Night Monkeys were kept in cages at the Smithsonian Institution laboratory on Barro Colorado Island between August 1958 and July 1963, for periods ranging from several months to more than 3 years. Some individuals were kept in small cages, 8' x 4' x 4', inside a house; but the majority were in larger cages outdoors in the forest. The outside cages varied in size from 6' x 6' x 8' to 30' x 12' x 8'. Generally each cage contained a single individual, a mated pair, or a family group; sometimes, however, larger groups (up to five individuals) were kept together in a large cage for a few days. All the Night Monkeys kept in captivity on Barro Colorado Island were wild-caught animals from mainland areas in Panama (probably, in most cases, from regions east of the Canal Zone) or were the offspring of such animals.

Some other captive Night Monkeys were observed briefly in the National Zoological Park, in Washington, D.C., in October 1959 and July 1960, and in Iquitos, Peru, in December 1958.

All observations of wild Night Monkeys were made on Barro Colorado Island, in both apparently mature and old second-growth forest (see Bennett, 1963).

The captive animals on Barro Colorado Island were sometimes observed from blinds; but such concealment usually was not necessary. Blinds were not used for observations of other captive individuals or the wild animals in the forest. Some of the captive individuals on Barro Colorado Island were accustomed to continuous but dim artificial light at night. This did not appear to affect their behavior after the first few nights. All other individuals were observed without using artificial light whenever possible. Sometimes moonlight was sufficient to reveal at least the most conspicuous and vigorous movements. Even in nearly complete darkness, it was sometimes possible to follow the behavior of the animals by the sounds of their movements and vocalizations. When artificial light was necessary, flashlights were used (either intermittently or continuously). This certainly affected the behavior of the animals, but did not always alarm them greatly or cause them to escape immediately.

According to Hershkovitz (1949), there is only one species of Night Monkey: *Aotus trivirgatus*; and the Panamanian population

belongs to the subspecies *griseimembra*. The exact provenance of the animals in the National Zoological Park in Washington, D.C., was unknown. The animals observed in Iquitos supposedly were caught in nearby areas and, therefore, were presumably representatives of the nominate subspecies (Herskovitz, *op. cit.*) or the possibly distinct subspecies *vociferans* (Cabrera, 1957).

All references to the behavior of other platyrrhine monkeys in the following pages are based upon personal observation, unless specifically stated otherwise.

GENERAL HABITUS, LOCOMOTION, AND FEEDING

Some characteristic activities of Night Monkeys in the wild have been described in a number of earlier publications. The best general survey is by Cabrera and Yepes (1940), who summarize the reports of many early naturalists and travelers in South America; and the best account of Night Monkeys in Panama is by Enders (1935). It may be useful to recapitulate some of this information, and add a few details about locomotory and feeding habits, before discussing other aspects of behavior.

Night Monkeys differ from all other "true" monkeys in being almost completely nocturnal. Both captive and wild individuals are most active immediately after nightfall and just before dawn.

Wild Night Monkeys sometimes start to become active in the evening before it is completely dark, and may continue to move about for some minutes after it has started to become light in the morning. Captive individuals easily learn to move about in the daytime, and their adjustment to continuous artificial light at night is usually rapid. They appear to see quite well in all but the brightest light. This is not surprising, as there is some evidence (see, for instance, Hill, 1957, and Rohen, 1962) that the nocturnal habits of Night Monkeys are specialized rather than primitive among Platyrrhini. (The terms "primitive" and "specialized" are used, throughout this paper, as defined by Simpson, 1961.)

Wild Night Monkeys apparently are purely arboreal. On Barro Colorado Island, they usually move and feed in trees at heights ranging from 20 to at least 100 feet above the ground, and apparently never come lower than 10 feet above the ground. During the daytime, they sleep in holes in trees.

The fur of Night Monkeys is very thick and soft. This softness may be an adaptation to nocturnal and arboreal habits, possibly helping to reduce or muffle the sound of movements. It is probably

not coincidental that such unrelated animals as Kinkajous (*Potos*), Olingos (*Bassaricyon*), and Woolly Opossums (*Caluromys*), which are also nocturnal and arboreal, have fur of similar texture.



FIG. 1.—Two typical semierect preleaping postures.

Night Monkeys are extremely active and agile. (Hill, 1956, says that they are fairly slow moving; but this is certainly not true of individuals in the wild or of healthy captive individuals in adequate cages.) Like monkeys of the genera *Callicebus*, *Pithecia*, and *Cacajao*, they are expert and powerful leapers. Rapid movements through the

trees are usually accomplished by great bounds. When leaping, most of the propulsive power appears to come from the hind limbs, the forelimbs being used chiefly to absorb the shock of landing. The long and rather heavy tail seemingly is used as a counterweight, never as a prop or support. (This is another resemblance to *Callicebus* and *Pithecia*.) Night Monkeys run along branches less frequently than monkeys of the genera *Cebus* and *Saimiri* or tamarins such as *Saguinus geoffroyi*. (The generic names used in this paper follow Hershkovitz, 1958.)

As noted by Hill (1957), Night Monkeys are among the most nearly completely quadrupedal monkeys. Not only do they usually use both fore and hind limbs in locomotion, but they generally grasp a supporting branch with one or both hands even when sitting quietly. Just before leaping, however, they may take their hands off the supporting branch and sit or stand in a semierect posture, balancing on the hind limbs alone (see figure 1). The hind limbs generally are flexed in this posture, the back may be nearly straight or curved to an appreciable extent, and the front limbs may hang downward or the hands may be slightly raised (presumably in preparation for grasping a branch after the leap). An individual may remain poised in this way for several seconds or more.

Night Monkeys seem to eat a great variety of fruits and insects under natural conditions, and learn to eat artificial foods without difficulty in captivity. Their method of approaching and "handling" nonmoving food in captivity is interesting. They generally begin by sniffing at the food. (For other indications that they may have a good sense of smell, see below.) After sniffing for several seconds, an animal usually will seize the food with its teeth, and then sit up. Only then, in most cases, will it raise one or both hands to hold and possibly manipulate the food as it begins to chew.

The various ways in which different species of platyrrhine monkeys use their hands and fingers have not been well described. Some incorrect statements and misinterpretations are current in some of the published literature. Sanderson (1957), for instance, states that Night Monkeys have opposable thumbs and use their hands in much the same way as human beings. In a later passage, he also implies that they usually oppose the first two fingers of the hand against the last three (in much the same way as monkeys of the genera *Pithecia* and *Alouatta*). Both statements are somewhat misleading.

Night Monkeys often spread their fingers more or less radially when grasping an object. At such times, all the fingers tend to diverge

from one another to approximately the same extent. At other times, all five fingers of the hand may be kept pressed closely together. When some appreciable opposition does occur, it is perhaps most common for the thumb to be opposed to the other four fingers as a group; but this is by no means always the case. I have, in fact, seen Night Monkeys arrange their fingers in every possible way when grasping objects of different sizes and shapes. The first two fingers may be partly opposed to the last three; or the first three fingers may be partly opposed to the last two; or the first four fingers may be opposed to the fifth.

It is quite probable that this type of hand and use of fingers is primitive among Platyrrhini. (The actual structure of the Night Monkey hand is described in detail by Biegert, 1961.)

The most important general feature of the social behavior of Night Monkeys is their slight degree of gregariousness. On Barro Colorado they are seldom found in groups larger than a single pair or a single family of two parents with one young.

ORDINARY GROOMING AND CLEANING ACTIVITIES

New World monkeys perform two types of grooming: Self-grooming and mutual or social grooming, *i.e.*, the grooming of one animal by another. The former type may be called "autogrooming" and the latter "Allogrooming." (These terms have been suggested by the terms "autopreening" and "allopreening" applied to birds by Cullen, 1963.)

Most monkeys devote considerable time and effort to autogrooming; but different species tend to do this in slightly different ways.

The autogrooming of Night Monkeys consists almost entirely of scratching with the hands and/or the feet. Only very rarely does a Night Monkey use its teeth during autogrooming to "nibble" at its own fur or skin. The relative frequency of different types of autogrooming movements performed by some adult and subadult individuals in captivity on Barro Colorado Island is shown in the accompanying tabulation.

The actual frequency of autogrooming movements may vary widely, depending upon the situation. Most of this variation seems to be a function of the amount of dirt or ectoparasites in the fur, or of its disarrangement. In captivity, however, it is evident that most adult individuals tend to perform fewer autogrooming movements, on the average, than young individuals. This may be because adults tend to be less tame than young individuals in captivity. Night Monkeys seldom, or perhaps never, perform autogrooming movements when

they are either aggressive or alarmed. In this respect, they are quite different from many other New World monkeys, *e.g.*, species of the genera *Alouatta*, *Ateles*, and *Cebus*, which tend to perform particularly frequent and/or vigorous scratching in such circumstances.

It is my impression that young Night Monkeys also may tend to perform relatively more scratching movements with their feet, and

TABULATION OF ORDINARY GROOMING AND CLEANING REACTIONS

<i>Autogrooming performance</i>	<i>Number¹ of bouts</i>
Scratching the face with one hand.....	23
—the side of the head with the hand of the same side.....	1
—the chest with one hand.....	1
—the side of the body with the hand of the same side.....	24
—one hind leg with the hand of the same side.....	19
—one foot with the hand of the same side.....	5
—the genital region with one hand.....	4
—the tail with one hand.....	4
—one arm or hand with the other hand.....	16
—the tail with both hands.....	3
—the chin with one foot.....	2
—the face with one foot.....	11
—the side of the head with the foot of the same side.....	1
—the chest with one foot.....	1
—under one arm with the foot of the same side.....	1
—one arm with foot of the same side.....	7
—the side of the body with the foot of the same side.....	17
Nibbling the fur of the tail.....	1
<i>Cleaning performance</i>	
Licking a hand.....	3
Rubbing the nose along the substrate.....	2

¹ This count is based upon observations of six individuals; two immatures and four adults. The longest period of observation of a single individual was 1 hour. The shortest period was 12 minutes.

relatively fewer scratching movements with their hands, than adults in similar situations. There may be two reasons for this: (1) Young individuals find it more difficult to balance with one hand off the ground and (2) they can reach most parts of their (relatively shorter) bodies with their feet more easily than can adults.

Unlike most other platyrrhines, Night Monkeys seldom perform allogrooming except in obviously sexual or partly sexual circumstances (see below). This presumably is correlated with their slight degree of gregariousness, but it is not due simply to lack of opportunity. Mated Night Monkeys rarely groom one another even when

they are close together if they are not also performing other sexual patterns.

A Night Monkey with dirt on its face sometimes removes the dirt by rubbing the face along a branch. These reactions are actually rare, but seem to be performed more frequently by Night Monkeys than by any other platyrrhines with which I am familiar except the tamarins of the genus *Saguinus*.

Night Monkeys clean their hands and fingers by licking.

The tabulation of autogrooming movements on page 7 also includes the cleaning movements performed by the same individuals during the same periods of observation.

HOSTILE BEHAVIOR

The term "hostile" may be applied to all behavior patterns resulting from a tendency to attack and/or a tendency to escape. In this sense, it is synonymous with the term "agonistic" as used in many other discussions of behavior (*e.g.* Scott, 1958).

The term "tendency" will be used in a broad sense throughout this paper, to designate any "readiness to show a particular type of behavior" (Marler, 1956).

In preliminary and essentially descriptive accounts of behavior based on observation rather than experiment, such as the present account of the Night Monkey, it is usually not necessary to distinguish between a great number of qualitatively different tendencies. Most social reactions can be characterized as the products of such broad tendencies as attack, escape, gregariousness, copulation, pairing, etc.¹

¹ The tendencies involved in the production of an otherwise ambiguous behavior pattern may be revealed by analysis of the other activities usually associated with the pattern. Conversely, the term "tendency" may provide a convenient and concise way of summarizing the circumstances in which a behavior pattern occurs. Thus, for instance, when a signal pattern such as a ritualized posture or a vocalization (see below) is said to be produced by the attack tendency, this means that an animal performing the pattern is likely to perform overt attack movements during or immediately after the pattern and/or give some outward indication that it "wants" to attack. When one signal pattern is said to be produced by a stronger attack tendency than another signal pattern, this means that the former is more likely to be accompanied or followed by overt indications of attack than the latter and/or is likely to be accompanied or followed by stronger indications of attack than the latter. (It should be stressed, in this connection, that when a particular behavior pattern is said to be produced by one or more particular tendencies it does not mean that other tendencies may not be activated in an animal performing the pattern at any particular time.)

This type of terminology has been criticized on various grounds. Among the most recent critics is Andrew (1963). The term "tendency" as used here is certainly a great oversimplification, but its convenience in actual practice may outweigh its disadvantages in theory. Most ethologists have been driven to use the same or a similar term, or the same concept in more or less disguised form, when describing a variety of different types of social behavior.

Andrew (*op. cit.*) suggests that all or most signal patterns of primates may be caused by "stimulus contrast." This is undoubtedly true—if "stimulus contrast" is defined broadly enough. But platyrrhine signal patterns are certainly not produced by a single range of qualitatively similar stimulus contrasts of differing strengths. Certain stimuli usually ("normally") provoke only sexual patterns, others generally provoke only hostile patterns, still others usually provoke only parental responses, etc. Thus the causation of platyrrhine signal patterns can be described in terms of stimulus contrasts only if distinctions are made between qualitatively different types of stimulus contrasts, *e.g.*, between hostile stimulus contrasts and sexual stimulus contrasts. It may be doubted if such a system is any more convenient or useful than the employment of terms such as tendency. It is certainly more difficult to use in descriptive passages. (And, in fact, Andrew himself does not use it consistently throughout his own description of primate signal patterns.)

All the vocal patterns cited in the following pages will be given names, such as "Moan," "Grunt," "Gulp," etc. These names are used purely for convenience. They are not meant to describe the acoustical properties of the sounds in detail; this will be done in the accompanying drawings of sound spectrograms. They are meant only to suggest that the sounds are somewhat similar (to human ears) to the common human and other everyday sounds called by the same names.

The term "sound" itself will be used in its ordinary, everyday sense throughout the paper.

All the hostile behavior patterns mentioned are those of adults, both males and females, unless specifically stated otherwise.

OVERT ATTACK BEHAVIOR

Night Monkeys are among the most aggressive New World primates. Adult individuals of the same sex usually fight savagely when put together in a cage. Adults of opposite sex, mates or potential mates, may not engage in violent fights, but they do direct a consider-

able variety of hostile patterns toward one another in at least some circumstances (see below).

This aggressiveness must be one of the factors keeping pairs and family groups apart in the wild. Captive adults of more gregarious species of the genera *Saimiri*, *Cebus*, *Ateles*, and *Alouatta* usually do not fight with one another as frequently or as vigorously as do Night Monkeys kept in similar conditions.

It is perhaps surprising, therefore, that overt fights between pairs and family groups of Night Monkeys seem to be relatively rare in the wild, at least on Barro Colorado Island. This seems to be due to the fact that different pairs or family groups simply do not come into contact with one another often. Each pair or family group seems to have its own territory or home range, in which it remains all or most of the time. (These territories or home ranges may be largely "traditional." Their boundaries may be established, originally, by means of disputes. Once established, the boundaries may be respected simply because the animals remember the results of the original encounters. If so, the territories of Night Monkeys on Barro Colorado Island are maintained in the same way as those of many birds occurring in the same area—see Moynihan, 1962a.)

(I have seen relatively large groups of wild Night Monkeys [including four or five individuals] only in the immediate vicinity of major food sources, *i.e.*, trees in fruit. In such cases, one pair or family group may have been so strongly attracted to the food that it crossed over the boundary of its territory or home range. Some of the individuals in these groups showed obvious hostility toward one another; and the groups always broke up within a few minutes.)

An aggressive Night Monkey may perform a variety of displays (see below) immediately before and/or after attacking; but the overt attack behavior itself is usually relatively simple.

An attacking individual usually begins by advancing, walking, slowly and cautiously toward its opponent. Then, when it has come close enough, it suddenly leaps forward and tries to bite the opponent and/or hit the opponent with its hands. This hitting is reminiscent of the jabbing of a human boxer. Usually two or three jabs are delivered with great rapidity one right after the other.

It is my impression that Night Monkeys strike with their hands during fights relatively more frequently than all or most other platyrrhines. This may be correlated with the fact that they do not have very long canine teeth.

A Night Monkey that has been attacked usually retreats as soon as possible; but its attacker seldom follows immediately. Even when

very aggressive, the attacker generally pauses a few seconds, before starting another slow and cautious advance, preparatory to another attack leap.

The Night Monkeys kept in captivity on Barro Colorado Island generally were quite silent while attacking; but once I heard an individual "spit," like a cat, at the very instant of jabbing an opponent. Hill (1960) mentions similar sounds in similar circumstances. So perhaps spitting sounds are a normal part of the attack behavior of Night Monkeys, at least in some populations of the species.

Sometimes two individuals will try to attack one another simultaneously. This may lead to a brief but extremely violent wrestling match, while each animal tries to bite and/or strike the other.

All these patterns, with the possible exception of "spitting," would appear to be expressions of the attack tendency alone. At least, they do not include any components that are unmistakable indications of any other tendency.

Other attack reactions may be less direct. It is not uncommon to see an aggressive animal leap over, or just to one side, of its opponent, instead of directly toward it. An aggressive animal leaping in this way is less likely to bite or strike its opponent than is an animal that has leapt more directly. In such cases, it would appear that the attack has been "deflected," probably by some counteracting tendency.

The tendency most likely to counteract attack during most hostile encounters is undoubtedly escape. There is considerable evidence that an escape tendency generally is activated to some extent, however slight, in all or most situations in which attack is activated. Even the most aggressive animals sometimes interrupt their attack behavior, by retreating briefly and/or performing displays which probably include an escape component.

Mated pairs of captive animals kept in adjacent cages may become engaged in vigorous disputes with one another. In such cases, it is obvious that usually males try to attack males while females try to attack females. Males also tend to attack more frequently, on the average, than do females.

Captive Night Monkeys seldom "redirect" (see Bastock, Morris, and Moynihan, 1953) attack upon individuals other than the ones provoking the attack. They certainly perform redirection attacks much less frequently than do individuals of many other species of *Platyrrhini* in similar circumstances. This seems to be due partly to the fact that direct expression of their aggressiveness is seldom or never impeded by any positively "friendly" gregarious tendency. Even

more important, mated Night Monkeys apparently never redirect attacks upon their mates or young.

This partial inhibition seems to be one of the more distinctive features of the behavior of Night Monkeys. It must be advantageous, and it may also be directly correlated with the social structure of the species. Although there is no proof, it seems likely that the pair-bonds of Night Monkeys are comparatively strong and stable. (At least, it is not uncommon to find two Night Monkeys in the same area of the forest, behaving in more or less the same way, for months at a time. It is difficult to believe that the individuals involved are not the same throughout the whole period.) Pair-bonds seem to be weaker and/or less continuous in some other New World primates, such as *Alouatta palliata* and *Cebus capucinus*, and the males of such species do perform redirection attacks upon females and young with considerable frequency (at least in captivity). There may have been strong selection pressure against such behavior in Night Monkeys simply because it is particularly important for them to avoid doing anything that might interfere with the maintenance of their pair-bonds.

The only redirection attacks observed during the present study were performed by one captive individual on Barro Colorado Island, when it was placed in a cage between two other cages that also contain Night Monkeys. When this individual became engaged in a dispute with one of its neighbors (fighting through the intervening wire mesh), it would occasionally interrupt the fight to make a rapid and absolutely unprovoked attack upon its neighbor on the opposite side.

I have never seen Night Monkeys jump up and down in rage, or shake branches of trees, or break off and drop branches, like so many other species of both New World and Old World monkeys (see, for instance, Carpenter, 1934 and 1935, Ullrich, 1961, and Hinde and Rowell, 1962). They may lack such patterns because they are rather small and light in weight.

Many other species of monkeys perform "play wrestling," all or most of which seems to be a type of partly inhibited attack. This also seems to be almost or completely lacking in Night Monkeys, presumably as another consequence of their slight degree of gregariousness. Even when several young Night Monkeys are kept together in the same cage, they do not perform any wrestling which appears to be anything but ordinary, uninhibited attack.

OVERT ALARM OR ESCAPE BEHAVIOR

The simplest alarm reaction of Night Monkeys is a brief "freeze." In the most common form of freeze, an animal remains motionless

in whatever posture it was in when it first perceived a disturbing stimulus. Such freezes tend to be performed as reactions to distant stimuli or familiar near stimuli. They are not usually associated very closely with vigorous movements or displays in such circumstances.

Sometimes an animal will close its eyes, briefly, immediately before, during, or immediately after pausing in a simple freeze.

The most conspicuous escape behavior of Night Monkeys in the wild or in large cages is simply rapid, running or leaping, retreat. This tends to be performed as a reaction to some strong, near and/or unfamiliar stimulus, such as actual attack or other overt aggressive behavior by another individual of the same species or the sudden approach of a "potential predator" such as a strange human being. Active retreats frequently are preceded and/or followed by elaborate displays.

In similar social circumstances, a Night Monkey in a *small* cage may either run or leap around its cage very rapidly or, alternatively, perform a pattern which is reminiscent of the simple freeze described above but somewhat more complex. In this pattern, the animal sits motionless with its head lowered (such lowering is not characteristic of ordinary freezes). The head is sometimes lowered almost to the level of the hands or the branch on which the animal is sitting. The animal may look straight down, or keep its head turned sideways in order to fixate the disturbing stimulus. At the same time, the limbs may be drawn in under the body and strongly flexed. This is obviously a preparation for (or an "intention movement" of) leaping. As a result of the lowering of the head, the back is more or less curved (but not raised). Some typical variations of this "head-down posture" are shown in figure 2.

It is possible that Night Monkeys also assume head-down postures in the wild under completely natural conditions. I never actually saw such reactions in the forest on Barro Colorado Island (they would be extremely difficult to distinguish in trees at night); but some of the animals kept in large cages, which approximated natural conditions, did assume head-down postures from time to time.

The captive individuals in large cages did not, however, assume head-down postures as frequently as individuals of many other species of platyrrhine monkeys in similar situations. And their head-down patterns were not as exaggerated in form as the homologous patterns of some related species.

All these overt escape or alarm patterns are usually silent. The fact that Night Monkeys customarily are silent during rapid retreats from potential predators is another distinctive feature of the species,

as all or most other platyrrhines utter special "Warning Notes" in such circumstances. It is probable, however, that the Night Monkey does have one pattern in its vocal repertory which is at least partly homologous with the Warning Notes of some other species, although uttered in a slightly different range of circumstances and subserving a different function (see discussion on page 43).

All the alarm and escape reactions of Night Monkeys would appear to be expressions of the escape tendency alone, in much the same way that the aggressive reactions described above seem to be expressions of the attack tendency alone. The circumstances in which the various patterns occur would suggest that simple freezes are produced by weaker motivation than either active retreat or head-down postures. The strength of the escape tendency may be approximately the same in the latter two patterns, the head-down posture being assumed only by individuals unable or unwilling to retreat, possibly for any one of several different reasons.

The head-down postures are the most interesting of these patterns from a functional point of view. Both head-downs and ordinary freezes seem to be primarily attempts to hide, and to hide the whole animal, *i.e.*, to prevent a potential opponent or predator from noticing any or all parts of the motionless animal. Some of the head-down patterns may also be advantageous in a slightly different way. When an animal in a head-down posture looks straight downward, its black and white facial pattern and its eyes usually are partly or wholly concealed. These facial features seem to be the characters that release attack most frequently, or toward which attacks are usually directed. Thus an individual in a head-down posture of this type may not be attacked by an opponent or (possibly) a predator, even though the rest of its head and body are perfectly visible, and have in fact been noticed. In such cases, the head-down may function as "appeasement," reducing the attack tendency of an opponent without increasing its escape tendency (see Moynihan, 1955). The closing of the eyes during some ordinary freezes may subserve a similar function, although presumably less effectively.

DISPLAY BEHAVIOR

The most common hostile behavior patterns of Night Monkeys are "displays."

The term "display" may be used to include all "ritualized" patterns, *i.e.*, all vocal patterns and all movements and postures that seem to have become specialized in form and/or frequency to serve signal



FIG. 2.—Four head-down postures.

functions. (This does not mean that all patterns that may function as signals are necessarily displays. The head-down and eye-closing patterns, for instance, may be functioning as signals when and if they appease, but there is no really convincing evidence that they have become specialized to serve such a function. They are not more frequent or exaggerated in form than might be expected of pure evasive or avoidance patterns.)

Following a common convention, the initial letters of apparently or certainly ritualized patterns will be capitalized throughout the subsequent account.

SWAYING

The captive Night Monkeys on Barro Colorado Island sometimes began to sway from side to side, instead of retreating or freezing, when they saw a predator or potential predator such as an ocelot or a human being some distance away. The Swaying movements were usually smooth, regular, moderately rapid, and extended over a fairly wide arc (*i.e.*, a Swaying animal would first lean several inches to one side of the vertical and then several inches to the other side). Sometimes an individual would sit on its haunches, grasping its perch with its hands, while it swayed. At other times it might stand up in a more or less extreme preleaping posture. In either case, the head might be kept facing straight forward or turned from side to side, the animal looking right as it swayed to the right and looking left as it swayed to the left.

Most Swaying was silent; but sometimes "Gruff Grunts" and/or "Gulps" (see below) were uttered at the beginning and/or toward the end of a bout of Swaying, especially when similar or identical sounds were uttered before and/or after the bout itself.

An animal performing very brief Swaying sometimes appeared to be doing nothing more than "peering" from side to side to get a better view of the disturbing stimulus; but most Swaying was much too prolonged and exaggerated and stereotyped in form to be serving this function alone. As exaggeration and stereotypy are characteristic of most displays in most species of animals, it seems probable that the Swaying of these Night Monkeys was ritualized. (The undoubtedly homologous Swaying of some other New World monkeys may be even more exaggerated in form and is undoubtedly ritualized.)

Unfortunately, the function(s) and, to a lesser extent, the causation of the Swaying of Night Monkeys remain partly obscure, primarily because the behavior was never observed in the wild.

One comment may be inserted here. Experience has demonstrated that ritualized patterns performed by captive individuals are always found to be part of the "natural" repertory of the species, performed by wild individuals under natural conditions, when it is possible to study the behavior of wild individuals in detail. This is certainly true for all the other New World monkeys that I have been able to observe at length both in captivity and in the wild. Captive animals may perform displays in situations that are different from those in which wild animals perform the same displays (see also below), but they do not perform displays that are not also performed by wild animals in some situations. Thus it is safe to assume that wild Night Monkeys also perform Swaying, although I did not actually observe it during my relatively brief observations in the wild.

The Swaying of the captive animals was frequently followed by overt escape. This, and the fact that it was apparently always provoked by the sight of a predator or potential predator, would indicate that it was produced by activation of the escape tendency. It seems likely, however, that some other tendency was also involved, as all or most other ritualized patterns of Night Monkeys and other species are produced when at least two tendencies are activated simultaneously. If so, the other tendency was probably attack, as some Swaying was accompanied by Gruff Grunts, and these notes certainly include an attack component (see below). If attack was activated during silent Swaying, it was obviously much weaker than escape, but it may have been relatively slightly stronger than in the previously described unritualized overt escape and alarm patterns. There was no indication of any significantly close or regular association between Swaying and any other type of social ("friendly" or sexual) behavior.

Swaying may discourage predators by letting them know that they have been seen. An alerted Night Monkey should have no difficulty in escaping from any natural predator. Night Monkeys are lighter, more rapid, and/or capable of leaping greater distances than any sympatric species of carnivore. Most of the individual carnivores in any given area must be well aware of this fact. Thus a carnivore that sees a Swaying (and obviously alerted) Night Monkey probably will not bother to chase it. This, in turn, means that the monkey will not have to waste time by escaping.

It seems likely that ritualized Swaying has been derived, in the course of evolution, from unritualized "peering." Some of the sideways components of Swaying may also have been derived from intention movements of turning away (from an alarming stimulus).

SILENT ARCH POSTURES

All the captive animals on Barro Colorado Island assumed distinctive "Arch Postures" quite frequently.

In these postures, the back was raised, usually to a considerable extent, and strongly arched or curved. The raising movement itself was always rapid, but the posture generally was maintained for an appreciable length of time (up to a minute in some cases). Sometimes an individual stood up on its hind limbs as it assumed an Arch Posture. In this case, the front limbs were allowed to hang downward, usually with the elbows more or less akimbo. Generally the hands were held with the backs facing inward and the palms outward and the hind limbs were straight or only slightly bent at the knees. A typical Arch Posture of this type is shown in figure 3c (such postures were quite similar to some semierect preleaping postures in many respects, but could always be distinguished by the more extreme curvature of the back). In other Arch Postures, the performing individual did not stand up, but remained clasping the perch with both hands and feet. In such cases, all four limbs were usually nearly straight. Typical Arch Postures of this type are shown in figures 3a and 3b. (It will be noticed that the relative positions of the head and back are nearly the same in both Arch Postures of this type and some head-down postures; but the effect is achieved by different methods in the two patterns, lowering the head in one case and raising the back in the other, and the general impression or "gestalt" of the two patterns is quite different.)

Irrespective of these minor variations in physical form, the Arch patterns of the captive animals could be divided into two main categories—one silent; the other accompanied by Resonant Grunts (see below).

Silent Arch Postures were assumed during all sorts of purely and partly hostile intraspecific encounters; but they were most common, and most long-sustained on the average, during the longest and most violent disputes between previously unacquainted individuals of the same sex and between "territorial" rivals in adjoining cages. They were often preceded and followed by a great variety of purely or partly hostile vocal patterns, produced by both attack and escape tendencies (see below), and/or by ambivalent unritualized hostile movements. When they were closely associated with an unambiguous unritualized hostile reaction, however, it was always overt attack, *not* escape. Individuals assumed silent Arch Postures with appreciable frequency both before and after delivering overt attacks.

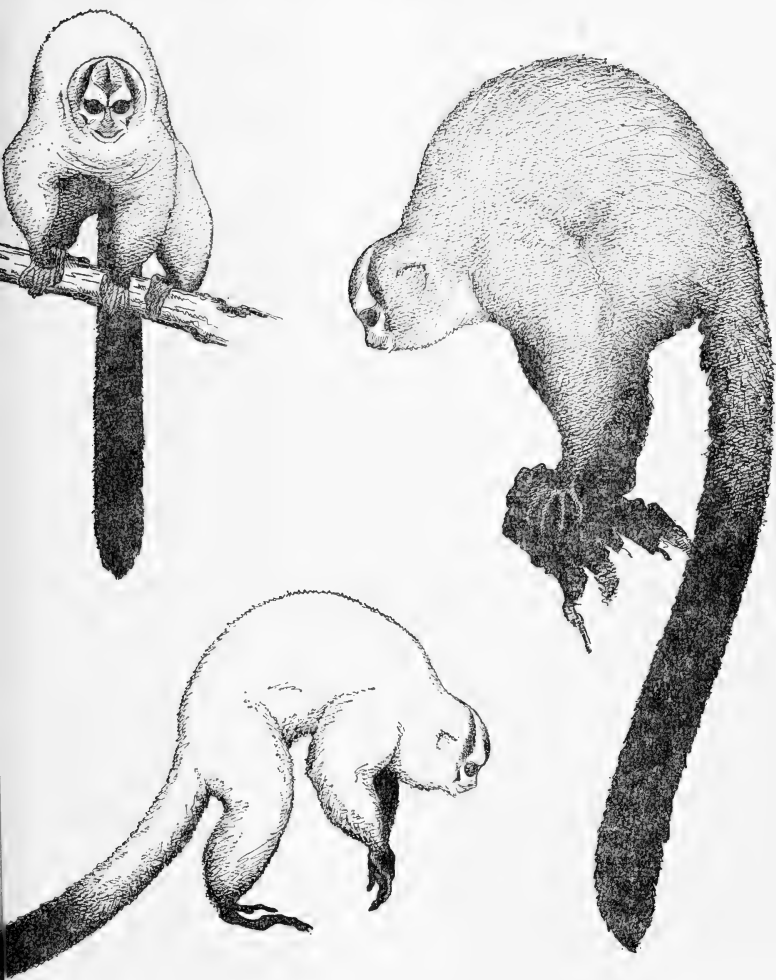


FIG. 3.—Arch Postures.

Upper left and right, two typical Arch Postures with hands grasping the perch. Bottom, an Arch Posture with hands raised off the perch.

These facts would suggest that all or most silent Arch Postures are essentially purely hostile *per se*, and usually are produced when hostile motivation is rather strong. The attack tendency must be stronger than the escape tendency in all or most silent Arch patterns, but probably relatively weaker than in actual overt attack.

Both morphological types of Arch Postures, standing up and with both hands and feet grasping the perch, were common during silent Arch performances.

(A relatively very few Arch Postures were accompanied by a few Gruff Grunts, Gulpes, and/or "Squeaks" [see below]. These performances appeared to be closely related to, perhaps nothing more than abnormal variants of, typical silent Arch performances. They may have been produced by motivation intermediate between that usually producing typical silent Arches and that producing the accompanying notes without Arches.)

Silent Arch Postures seem to function as threat. The assumption of an Arch Posture by one individual during an intraspecific dispute usually induces retreat by its opponent. The sight of an Arch Posture apparently activates or stimulates the escape tendency (and probably suppresses or weakens the attack tendency) of the perceiving individual. This effect is probably partly due to the fact that an animal in an Arch Posture looks larger than usual.

The Arch Posture is particularly interesting from a comparative point of view. The only other New World primate known to have a similar pattern is the howler *Alouatta palliata*.

Part of the Arch Posture may have been derived from an intention movement of leaping. Even when it does not assume a semierect posture, a Night Monkey usually "shifts" its body backward, to put more of its weight on its hind limbs, just before leaping for any reason in any circumstances; and this shifting tends to increase the normal curvature of the back. The straightening of the limbs in the Arch may have been derived from another source. Many other platyrrhines (*e.g.*, *Cebus* spp.) tend to hold the limbs very straight and stiff when jumping up and down in rage. It is conceivable that the Night Monkey has retained the "stiff-leggedness" of such a pattern, even though it has lost the jumping component. At least, I have never seen similar straightening of the limbs by any other species (except *Alouatta palliata*) in other circumstances.

OTHER VISUAL PATTERNS

An important negative feature of the hostile repertory of Night Monkeys is the comparative rarity of "displacement" activities, *i.e.*,

activities that appear to be "irrelevant" or "extraneous" or "out of context." Individuals of this species seem to perform such activities relatively much less frequently than individuals of many related species.

The absence or extreme rarity of autogrooming in hostile situations has already been mentioned.

There is only one pattern that may be partly equivalent to the "displacement" scratching of many other platyrrhines. Some of the captive Night Monkeys on Barro Colorado Island sneezed repeatedly during some high-intensity disputes. In other situations, sneezing seems to be a cleaning or comfort movement of a peculiar type used to clear or clean out the nose. Sneezing is very common after feeding, presumably because animals tend to get food up their noses. As the Night Monkeys that sneezed so frequently during disputes had not been feeding immediately beforehand, it is at least conceivable that some or all of their sneezing was a direct result or consequence, in one way or another, of their hostility.

(The whole problem of "displacement" activities by New World primates will be discussed in a later paper.)

Night Monkeys defecate and urinate in some hostile situations. A captive but untamed individual may defecate and/or urinate when caught and picked up by a human being. This is usually accompanied by "Screams" (see below) and/or Gruff Grunts. Some or all of these defecation and urination patterns are probably produced when both attack and escape tendencies are strong, but escape is definitely predominant over attack.

I do not think that the defecation and urination patterns of Night Monkeys subserve any signal function or help to repel predators at a distance. Wild individuals of many other species of New World monkeys frequently urinate and/or defecate upon predators or potential predators passing beneath them in the forest; but none of the wild Night Monkeys on Barro Colorado Island was observed to do so.

Vomiting may also be closely associated with the hostile behavior of Night Monkeys in certain circumstances. Some of the captive individuals on Barro Colorado Island vomited occasionally, or performed the "heaving" motions that frequently precede vomiting, during or immediately after hostile reactions (escape movements, Swaying, and/or Gruff Grunts) to the approach of a human observer.

Night Monkeys have fewer signal patterns designed to be perceived by the eye than many other New World primates; and most of the signal patterns of this type that they do have are comparatively crude or "gross," produced by simple movements of the whole body and/or

head. They lack the variety of facial expressions (*e.g.*, frowns, baring of teeth, pursing of lips) which are important signal patterns in such platyrrhines as *Cebus* and *Ateles* species. They also lack the special elongated tufts and ruffs of hair on the head and around the face which are typical of many marmosets and tamarins, and which can be erected or depressed to convey signal information. The absence of such characters may be correlated with nocturnality. Adult Night Monkeys frequently become separated (by distances of at least several yards) from their mates and subadult young while feeding and moving in the forest at night. In such circumstances, they probably cannot rely upon perceiving visual signals, especially small and complex signals, from their companions as frequently or as easily as can adults of other platyrrhine species which are diurnal or crepuscular (see also discussion on page 45).

Andrew (*op cit.*) says that Night Monkeys open the mouth in threat. I never saw this except when sounds were uttered at the same time.

The complex black-and-white head pattern of Night Monkeys (more complex than the corresponding patterns of any other New World primate) may provide a partial substitute for a variety of facial expressions, whenever Night Monkeys are close enough together to perceive the pattern clearly. Because the black and white stripes and patches are convergent and divergent, and some of them are curved, a slight alteration of the position of the head relative to an observer will tend to alter the whole appearance or "gestalt" of the pattern (see the accompanying sketches). This must help to emphasize the signal effect of head movements.

GRUFF GRUNTS

Most of the vocal patterns of adult Panamanian Night Monkeys can be divided into eight main categories: Gruff Grunts, Resonant Grunts, Screams, Low Trills, Moans, Gulps, Sneeze-grunts, and Hoots. All except the last seem to be purely or partly hostile.

Gruff Grunts are among the most common of the vocal patterns. I heard them uttered by both wild and captive individuals on Barro Colorado Island and by all the other captive individuals studied. The typical Gruff Grunts of almost all individuals were similar or identical in sound (to the human ear), low-pitched, moderately long, and moderately loud. Figure 4 is a sketch of a sound spectrogram of a single note of this type.

(All the sound spectrograms illustrated in this paper are derived

from recordings of captive individuals on Barro Colorado Island. The recordings were made by an Ampex 601, using an Electrovoice 666 Variable D Cardioid microphone.)

Gruff Grunts usually are uttered singly or in short series of two to five notes. Each note of a short series seems to be essentially the same as a single note, and the successive notes may be uttered at slightly irregular intervals. Series are frequently repeated, but successive series generally are separated by relatively long pauses (much longer than the longest intervals between notes of a single series).

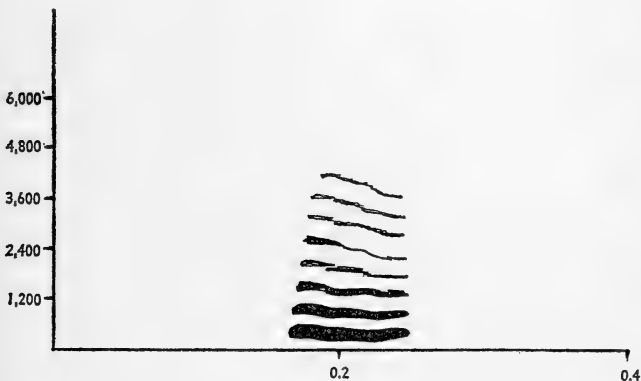


FIG. 4.—A typical Gruff Grunt, uttered by an adult.

Based upon a sound spectrogram made by a Kay Electric Co. "Vibralyzer."

In this and all the following sketches of vocal patterns, the figures along the vertical axis indicate cycles per second and the figures on the horizontal axis indicate elapsed time in seconds.

All Gruff Grunts seem to be uttered with the mouth almost or completely closed; but they are usually, or perhaps always, accompanied by conspicuous inflation of the throat region, the throat swelling up just as a note begins, and then subsiding immediately as soon as the note ends (even when the note is part of a series).

Both single Gruff Grunts and short series of such notes are uttered frequently during all sorts of hostile encounters, apart from partly sexual situations, during both brief and prolonged intraspecific disputes in the wild as well as in captivity, and as reactions to the appearance of a predator or potential predator. During intraspecific disputes, they are uttered by aggressive individuals before and after

attacking, by obviously frightened or defensive individuals before and after performing overt escape movements, and by individuals that perform both overt attack and escape movements as well as other displays. They are also uttered during some encounters between mates or potential mates (see below), but they are relatively (if not always actually) uncommon in such circumstances. These facts would suggest that all or most Gruff Grunts are produced by simultaneous activation of the attack and escape tendencies, and these tendencies alone. The range of motivation is probably quite broad. Some Gruff Grunts seem to be produced when the attack tendency is appreciably stronger than the escape tendency; others when the escape tendency is appreciably stronger than the attack tendency; and still others when the two tendencies are effectively equal. The attack tendency probably is never as preponderant during any Gruff Grunt performance as during silent overt attack movements; and the escape tendency is probably never as preponderant during any Gruff Grunt performance as during silent overt escape movements or simple freeze or head-down patterns. The actual strength of the two tendencies involved may be quite different in different circumstances. Some of the single Gruff Grunts and short series of such notes during brief disputes probably are produced when both tendencies are actually weak. Some of the similar-sounding series of notes during prolonged and vigorous disputes may be produced when both tendencies are actually quite strong. The escape tendency may be relatively weaker during the least aggressive typical Gruff Grunt performances than during silent Swaying; or, if the relative strength of the two hostile tendencies is the same in the two types of performance, their actual strength may be greater during the Gruff Grunts than during silent Swaying. Similarly, the most aggressive Gruff Grunt performances may be less aggressive than typical silent Arch Postures or, perhaps less probably, produced when the total actual strength of the hostile motivation (the attack and escape tendencies together) is less than in the silent Arches.

Gruff Grunts certainly function as threat during intraspecific disputes. They probably do not have a regular signal function when provoked by the appearance of a potential predator.

Some of the captive individuals on Barro Colorado Island were heard to utter single but frequently repeated soft notes which sounded as if they might be nothing more than weak or muffled versions of typical Gruff Grunt notes. Some of these were so soft that they were little more than audible expirations of breath. They were uttered by untamed individuals watching me approach, and were followed (when I came closer) by moderately vigorous escape movements, sometimes

with Gulps and/or Sneeze-grunts. They may have been produced by weaker hostile motivation than typical Gruff Grunt performances and have contained a relatively stronger escape component. (The difference in causation between these soft Grunts without Swaying and silent Swaying with typical Gruff Grunts was not clear.)

RESONANT GRUNTS

Resonant Grunt performances are much more complex in form than typical Gruff Grunt performances, and seem to be much rarer.

All the Resonant Grunts heard were uttered in long series of at least 10 to 15 notes. The speed, loudness, and pitch of the notes varied considerably.

The most frequently heard, and simplest, type of series was as follows. The first notes were soft and low, much softer than typical Gruff Grunts but otherwise similar. Succeeding notes gradually became louder and louder throughout the first half of the series. By the middle of the series, they were often very loud indeed, much more so than any Gruff Grunts, and had developed a penetrating, resonating quality. They were still gruntlike (insofar as they retained a guttural "rrrr" sound), but they had also acquired an "ooo" sound slightly reminiscent of the Hoots (see below). All the notes during the first half of a series were always uttered exceedingly rapidly one right after the other, in an emphatic "pumping" rhythm. The intervals between successive notes were much shorter than the intervals between notes in typical series of Gruff Grunts. It is possible that the pitch of the successive notes gradually became higher during the first half of some of these Resonant Grunt series, but this change (if it actually occurred) was always slight. Once the climax of a series was reached, the next few notes remained essentially similar, loud, resonating, and rapid. Then, during the final quarter (approximately) of the series, the rhythm usually slowed down a little and, at least in some cases, the notes became successively lower and/or softer.

Series of this type were heard only among the captive individuals on Barro Colorado Island. One male uttered 30 to 40 series during a violent dispute with neighbors in adjoining cages immediately after being reintroduced into a cage with which he was thoroughly familiar after an absence of several weeks. One female uttered one series toward the end of a long and violent dispute with a male to whom she had just been introduced. Another female, alone in her cage, uttered several series after being disturbed by a human being, just *after* the human being had left and disappeared from her sight. These three individuals uttered their series of Resonant Grunts at night; and they

certainly were not aware that their performances were being observed by a human being (from a blind). A very tame hand-reared male kept in a cage in the animal house, with a female to whom he was well adjusted, frequently uttered similar series at night and (more frequently) in the morning well after dawn, usually just as or just after an animal-keeper passed by his cage and/or some howler monkeys (*Alouatta palliata*) in an adjacent cage uttered "barks" and/or "roars" (see below).

The simple series of all these individuals except the solitary female were composed of essentially monosyllabic notes. At least some of the notes of the solitary female were definitely bisyllabic. Unfortunately, it was not possible to record any of these performances. The series of monosyllabic notes might be transcribed by something like

"Roo roo roo roo . . ."
rr rr rr rr

while the series of bisyllabic notes were something like

"Rooa rooa rooa rooa. . ."
rrr rrr rrr rrr

In all these performances, the individual uttering the Resonant Grunts assumed a moderate or extreme Arch Posture as soon as it began a series and went out of the posture as soon as the series was ended. Most of these postures were identical with typical silent Arches, with both hands and feet grasping the perch. The male engaged in disputes with his neighbors, however, tended to stand up on his hind limbs when he assumed an Arch. During some or all of these standing postures, his arms hung downward as usual but his elbows went in and out in rhythm with the accompanying notes. I think that the elbows always went in as a note was uttered and out between notes. Night Monkeys have a large ventral air-sac communicating with the larynx (Hill, 1960). It is possible that the inward movements of the elbows helped to expel air from the sac and that the outward movements helped to draw air into the sac. This may have facilitated sound production. (The other individuals were able to utter similar and probably equally loud notes without similar movements; but they did not utter as many series of notes in a short period of time.)

All these series of Resonant Grunts were immediately preceded by more or less prolonged periods of intense activity, the performing animal running and leaping madly about its cage and uttering many Gruff Grunts, Gulps, and Sneeze-grunts (and sometimes Moans and/or Low Trills).

The tame captive male occasionally uttered series of Resonant Grunts which continued to accelerate throughout. In some cases, these series ended in a "bubble" of very, very short rapid notes. In other cases, they accelerated to such an extent that the terminal notes "ran together," to form a continuous or semicontinuous and moderately loud "Roar." Both types of accelerated series were uttered in the same circumstances as the simpler series of the same male, in association with the same other patterns.

Dr. John H. Kaufmann (personal communication) heard one or more wild Night Monkeys on Barro Colorado Island utter Roars which may have been the culmination of similar accelerated series of Resonant Grunts. These patterns were uttered during a prolonged dispute between two pairs or family groups feeding, or attempting to feed, on a palm tree in fruit. Unfortunately, the postures and movements accompanying the notes were not observed. I heard two series of Resonant Grunt-like notes apparently uttered by wild Night Monkeys on Barro Colorado, again without being able to see the animals while the calls were uttered. The first series was composed of from 10 to 15 moderately loud and long bisyllabic grunts, all essentially similar and very low in pitch. The second series followed shortly after the first, and included many more notes. The notes were monosyllabic, and the series rose and fell in pitch at least twice. The general effect was almost singing. These series were probably uttered by one or both members of a mated pair, just before retiring to their sleeping hole at dawn. I could not determine what (if any) external stimuli provoked the performances.

With these few and enigmatic exceptions, Resonant Grunts were not heard to be uttered by wild Night Monkeys on Barro Colorado Island. It is possible that I missed many Resonant Grunt performances (see below), but I was out in the forest frequently enough to establish that such performances must at least be relatively very rare on Barro Colorado.

The association of Resonant Grunts with Arch Postures, their similarity in sound to undoubtedly hostile Gruff Grunts, and their occurrence during some disputes, would indicate that they are at least partly hostile. Although some Resonant Grunts show a slight resemblance to Hoots, and the latter are undoubtedly sexual (see below), none of the individuals observed to utter Resonant Grunts appeared to be sexually aroused at the time. They did not perform any overt pairing or copulatory reactions. This would suggest that all Resonant Grunts may be purely hostile. The rarity of Resonant Grunts, the complex forms of the series of such notes, and their close association

with periods of intense activity and obvious excitement would suggest that they are very high intensity patterns, produced when the total hostile motivation is very strong. They probably are higher intensity on the average than either typical Gruff Grunts or typical silent Arch performances. They certainly appear to be much more closely associated with, or confined to, periods of intense excitement than either of the latter patterns. Approximately half of the Resonant Grunt performances of the male engaged in disputes with his neighbors were followed immediately by his performing overt attack. The remainder were followed by a variety of ambivalent movements and/or other vocal patterns, all or most of which probably included an escape component, but never by actual, complete, overt escape. It may also be significant that the only captive individual that uttered Resonant Grunts while obviously aware of being watched was the very tame hand-reared male, the only individual that was not at all afraid of human beings. These facts would indicate that Resonant Grunts are at least as aggressive, on the average, as the most aggressive Gruff Grunts or (more probably) silent Arch patterns. (In other words, the preponderance of the attack tendency over the escape tendency may be as great in Resonant Grunt performances as in silent Arch postures, although the actual strength of both tendencies is greater in the former than in the latter.) The escape component may be almost as minimal in some Resonant Grunt performances as in some overt attack patterns, especially the "deflected" attacks.

The complete Resonant Grunt performances of the captive male engaged in disputes with his neighbors appeared to function as threat; but it was impossible to distinguish between the signal effects of the notes themselves and those of the accompanying Arch Postures.

The Resonant Grunt performances are reminiscent of the most spectacular vocalizations of some other platyrrhine monkeys. In particular, they sound much like some calls of titi monkeys, *Callicebus* spp., and the howler *Alouatta palliata*. The former have not been studied in sufficient detail to permit discussion of probable homologies and analogies; but the situation is clearer with respect to the latter. The Roar at the end of some series of Resonant Grunts seems to be strictly homologous with the loud and prolonged vocalization of *Alouatta* spp. which is responsible for the vernacular name of the genus. In the case of *A. palliata*, this is the pattern which Carpenter (1934) calls "type 1 vocalization" and describes as "a voluminous barking roar," and which Altmann (1959) calls the "roar or howl, type A1." It often sounds like nothing more than a much amplified and prolonged version of the Roar of the Night Monkey, and is frequently

preceded by barking or loud grunting noises which may be largely or completely homologous with typical Resonant Grunts. At low intensities of motivation, male *A. palliata* may utter series of similar or identical sounds (probably the notes that Altmann calls "male bark, type C1" and "incipient male bark, type C2") without ever breaking into an actual roar. Some of the lowest intensity and softest versions of such series, when heard at a distance, are remarkably difficult to distinguish from the simplest series of Resonant Grunts heard close up.

The resemblance between the two patterns is so great that the tame male Night Monkey had been uttering Resonant Grunts occasionally for several weeks before I realized that they were not being uttered by the howlers in the adjacent cage.

It has already been mentioned that the Resonant Grunt performances of this tame Night Monkey were sometimes uttered during or immediately after roars and barks by the adjoining howlers. Possibly they were directly released by the sound of the latter. If so, this would help to explain why this Night Monkey tended to utter Resonant Grunts in the morning rather than at night.

The apparent facilitation of Resonant Grunts by the roars and barks of howlers might be additional evidence that the patterns are related to one another.

(Although individuals of *A. palliata* may assume Arch Postures while uttering certain types of barks, they apparently do not usually assume such postures while uttering roars or the barks most closely associated with roars.)

The roars and barks of *A. palliata* are certainly hostile. Individuals of this species tend to associate in bands; each band seems to have its own home range or territory; and members of different bands usually utter roars and/or barks whenever they come close together (see Carpenter, 1934, and Collias and Southwick, 1952). If the Resonant Grunts of Night Monkeys are provoked by similar stimuli, the rarity of such notes in the forest on Barro Colorado Island may be partly due to the rarity of encounters between different pairs and family groups (see page 10). The roars of *A. palliata* apparently also function as long-range proclamations of territorial ownership (see Altmann, *op. cit.*), and are uttered quite regularly apart from close-range or face-to-face encounters with rivals or neighbors. It seems very unlikely that the Resonant Grunt performances of Panamanian Night Monkeys can serve a similar function with any appreciable frequency.

(It is possible, however, that some of the same or closely related patterns may do so in other populations of Night Monkeys. Hill,

1960, cites several descriptions and transcriptions of calls uttered by South American Night Monkeys which may be Roars or typical Resonant Grunts or similar notes. There are enough records of such calls to suggest that they may be common among South American populations. It is conceivable that the typical Resonant Grunts and/or the Roars are becoming "obsolescent," in process of disappearing, among Panamanian Night Monkeys.)

Some of the Resonant Grunt performances of Panamanian Night Monkeys may function as "triumph ceremonies" in certain circumstances. The performances by captive individuals *after* being disturbed or irritated, when the cause of the disturbance was leaving or had left, appeared to be "proclamations" of the fact that the performing individuals had defended their territories successfully.

(It is possible that Night Monkeys have some sort of "territorial motivation," a tendency which is satisfied by the possession of a territory, in addition to the ordinary attack tendency (see page 53). This might be involved in the causation of some Resonant Grunt performances. If so, it might help to explain why Resonant Grunt performances in which escape seems to be minimal do not always lead to immediate attack.)

Intermediates between typical Resonant Grunt and typical Gruff Grunt performances do occur, but apparently are always rare. I heard such intermediates only three times. All took the form of series of notes. Each note was similar to an ordinary Gruff Grunt in loudness and tone, but the successive notes of each series first rose and then fell in pitch in much the same way as in typical Resonant Grunt performances. One series of this type, including a great many notes, occurred in the same dispute in the forest on Barro Colorado Island in which typical Resonant Grunts also were heard. It was not possible to see the postures and movements accompanying this performance. A similar series was uttered by one member of a captive pair on Barro Colorado when disturbed by some stimulus (possibly an ocelot?) outside its cage. This was uttered from a crouch posture. Several shorter series were uttered by the mate of the captive male who uttered typical Resonant Grunts while engaged in disputes with his neighbors. She usually started a series just after the male had begun a series of Resonant Grunts, or just after he had finished—thus providing a peculiar "echo" to his performances. Her series were uttered from typical Arch Postures, with both hands and feet grasping a perch.

SCREAMS

The captive Night Monkeys on Barro Colorado Island and at Iquitos usually uttered loud Screams when caught and handled by a human being. (I presume that all Night Monkeys are capable of uttering similar or identical sounds; but none of the other individuals studied was caught and handled.) These Screams were always high pitched but wavering. Many of them were quite prolonged. Figures 5 and 6 are sketches of sound spectrograms of two typical Screams.

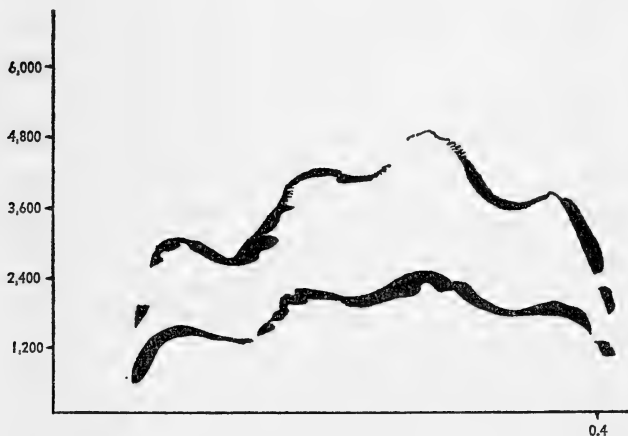


FIG. 5.—A relatively short Scream, uttered by an adult.

Based upon a spectrogram by a "Vibralyser."

Only the first harmonic is shown. There certainly was at least one other present.

All the observed Night Monkey Screams were uttered with the mouth wide open, but they were not accompanied by any conspicuous inflation of the throat region.

All the captive animals struggled violently when first picked up. Most of the struggling movements were obviously attempts to escape; but many of the animals also tried to bite their captors whenever possible. The animals usually uttered many Screams during the initial struggles, when both their escape movements and attempts to bite were most vigorous. If the animals were held firmly for several minutes, however, they usually calmed down, gradually, and their struggles subsided. At this stage, they generally stopped Screaming and started to utter Gruff Grunts and/or Gulps.

These facts would indicate that the Screams were produced when hostile motivation as a whole was very strong, when the escape tendency was much stronger than the attack tendency (although probably less preponderant than in the silent overt escape and alarm patterns). The actual strength of the hostile motivation as a whole during Screams was almost certainly greater than in any Gruff Grunt pattern in which escape is predominant.

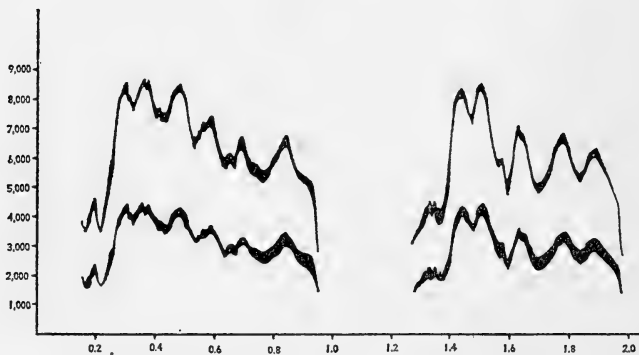


FIG. 6.—Two long Screams, uttered by an adult.

Based upon a spectrogram by a Kay Electric Co. "Sona-graph."

Only the first harmonic is shown. There was at least one other with each note.

In this and all the following sketches which include more than one note, the interval(s) shown between notes are the actual interval(s).

Screams may be adapted to frighten or startle a predator, and thus give a screaming animal a better chance to escape.

LOW TRILLS

Night Monkeys utter a variety of sounds that can be described as Trills.

The most common sounds of this type uttered by captive adults on Barro Colorado Island were "Low Trills." A single Low Trill was a "bubbling" series of short low-pitched notes, uttered *very* rapidly one right after the other but still distinguishable by the human ear. All or most of the individual notes in a series were slightly plaintive in tone, and sounded somewhat like abbreviated versions of simple Moans (see page 36). The number of notes in a single series varied

from three to at least twelve. The successive notes tended to rise slightly in pitch. Sketches of sound spectrograms of three more or less typical Low Trills are shown in figures 7, 8, and 9.



FIG. 7.—A Low Trill, uttered by an adult.

Based upon a spectrogram by a Kay Electric Co. "Missilyzer."



FIG. 8.—One Moan, followed immediately by one Low Trill, uttered by an adult.

Based upon a spectrogram by a "Missilyzer."

All Low Trills were uttered with the mouth closed or nearly closed. They were not accompanied by any conspicuous inflation of the throat region.

They were uttered in several different situations. They were com-

mon during the initial reactions between strangers, previously unacquainted individuals meeting one another for the first time. In such circumstances, they could be uttered by any one or all of the individuals involved. When the previously unacquainted individuals were of opposite sex, females tended to utter Low Trills more frequently than males. Almost all individuals meeting a stranger tend to be very cautious at first, moving in a hesitant and apparently slightly alarmed manner. Females usually are even more hesitant than males. The Low Trills during initial "greetings" often were

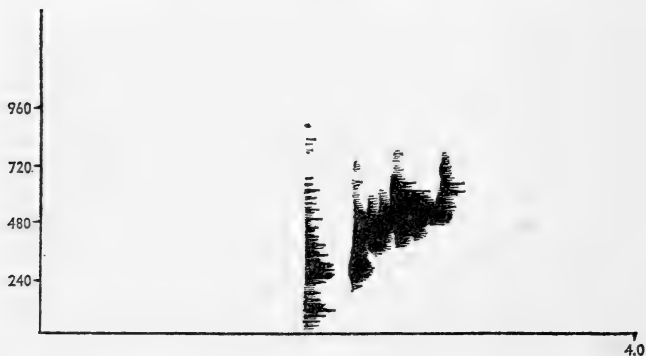


FIG. 9.—One Sneeze-grunt, followed immediately by one Low Trill, uttered by an adult.

Based upon a spectrogram by a "Missilyzer."

uttered in close association with, immediately before, or during "social sniffing" performances (see page 47). Similar notes were uttered frequently by single individuals immediately after being released in new cages, as they began to explore their quarters in a cautious manner. Some individuals also uttered such notes when they went down to get food from dishes on the ground, even when they were in familiar quarters and/or there were no other Night Monkeys nearby. Captive Night Monkeys tend to be slightly "nervous" whenever they have to come down to the ground, presumably because they would never do so under natural conditions. Although many Low Trills during "greetings" were eventually followed by overt, unritualized, hostile, and/or sexual behavior (depending upon the age, sex, and condition of the individuals involved), they were not usually uttered during or after

either actual fighting or copulatory reactions. The only prolonged and vigorous dispute during which I heard such notes uttered was an encounter between a male and a female that had fought with one another previously, been separated for several days, and then were brought together again.

These facts would suggest that many or all of the Low Trills were partly hostile reactions, produced when the escape tendency was stronger than the attack tendency, but effectively counteracted by some other nonhostile tendency, such as sex or feeding, or a non-hostile tendency plus attack. The nonhostile tendencies involved probably were not direct causes of the Low Trills in the same way as the escape tendency, as different nonhostile tendencies were involved in different situations while the sounds themselves remained essentially the same in all situations.

Some of the circumstances in which Low Trills were uttered were similar to those in which many other species perform appeasement displays. The Low Trills may have had a similar function; but I could not distinguish their exact signal effects from those of associated patterns such as social sniffing.

Two full-grown Night Monkeys at the National Zoological Park in Washington, D. C., and some apparently full-grown individuals in the forest on Barro Colorado Island were heard to utter Trills reminiscent of typical Low Trills in sound but higher pitched, more mechanical or metallic in tone, and without any plaintive or moaning quality.

The significance of these patterns was difficult to assess, as the captive individuals in the National Zoological Park were observed briefly and the wild individuals on Barro Colorado uttered their notes in obscure and/or complex social situations.

The National Zoological Park animals were a male and a female. I was told that they had been placed together in the same cage only a few days before my observations. They uttered their high-pitched Trills whenever they came face to face. Many of their Trills were followed by social sniffing, without any (other) overt indications of hostility. I did not hear them utter anything more closely similar to the Low Trills of the captive adults on Barro Colorado. This might suggest that their high-pitched Trills were equivalent to the latter, produced by the same or very similar motivation and serving the same function(s).

Unlike the Zoo animals, the wild Night Monkeys that uttered high-pitched Trills were also heard to utter typical Low Trills during the same social encounters.

I think that the high-pitched Trills of all these animals were very similar to, or even identical with, the High Trills of young Night Monkeys in sound (see page 69).

It is possible, therefore, that the apparently full-grown individuals heard to utter such Trills were really immature, in spite of their size, or had reverted to juvenile or infantile behavior for some reason (see discussion, page 58). It is also conceivable that high-pitched Trills are the only pattern of this type in the population from which the National Zoological Park animals were obtained.

As indicated in the accompanying figures, the notes of Low Trills are usually or always slightly higher in pitch than simple Moans. This might be evidence that Low Trills have been derived, in ontogeny and/or phylogeny, from a combination of typical Moans and High Trills.

Some or all Low Trills seem to have a slightly "liquid" quality, somewhat reminiscent of Gulp notes. There may be some sort of special relationship between the two types of patterns, either direct or indirect via the Gruff Grunt patterns (see both the accompanying figures and the comments below). Gulps, Moans, and Low Trills are all similar in some aspects of motivation.

MOANS

Many of the wild Night Monkeys on Barro Colorado Island and almost all the captive individuals at the National Zoological Park and at Iquitos as well as on Barro Colorado were heard to utter brief, soft, plaintive-sounding Moans (see figures 8 and 10).

Like the Low Trills, the simple Moans were uttered with the mouth apparently closed and were not accompanied by conspicuous inflation of the throat.

All or almost all the animals uttered Moans more frequently than Trills on the average. They uttered Moans in all the situations in which Low Trills were characteristic, and in other circumstances as well. Moans were relatively rare during the initial "greetings" between strangers and during the exploration of strange surroundings; but they were uttered frequently by individuals in familiar social and physical environments. They were the most common notes uttered by particularly tame (hand-raised) captive animals on Barro Colorado Island when I came within a few feet of their cages. At such times, they were uttered by animals approaching me in an apparently friendly or "curious" manner, as well as by animals performing slight retreat movements or intention movements. They were also uttered by mated

animals in captivity on Barro Colorado Island, if the mates were well adjusted to one another, when one individual rejoined its mate after being separated from it for a few seconds or minutes (the individuals that uttered Moans in such circumstances were long past the stage of uttering Low Trills as "greetings"). Moans were not usually directed by one individual toward its mate in other circumstances, *i.e.*, after they had been together for more than a few seconds. (The only exceptions were a few Moans uttered during the first parts of



FIG. 10.—One Moan, uttered by an adult.

Based upon a spectrogram by a "Missilyzer."

long precopulatory sequences. The animals that uttered these notes did not utter more Moans immediately before or during the actual copulations.) Some captive individuals on Barro Colorado Island uttered Moans while they watched other individuals fight without becoming involved in the fights themselves. A few individuals at both Iquitos and Barro Colorado kept in cages with monkeys and marmosets of other species but with no other individuals of their own species uttered Moans regularly as they moved about their cages in an almost perfectly relaxed manner. The other vocal patterns with which Moans were associated most frequently were Low Trills, Gulps, and Sneeze-grunts; *i.e.*, an individual that uttered Moans was quite likely to utter one or more of these other sounds immediately before and/or after the Moans. Both the Gulps and the Sneeze-grunts seem to contain

an escape component, at least at times (see below). Moans also were associated with Gruff Grunts, but relatively rarely.

It is probable, therefore, that Moans are similar to Low Trills in being produced when both hostile and one or more types of nonhostile motivation are activated simultaneously; but the hostile component seems to be relatively (and probably actually) weaker in the Moans than in all or most Low Trills.

Moans may also function as appeasement.

"LOCOMOTORY NOTES"—GULPS AND SNEEZE-GRUNTS

These two types of notes are among the most enigmatic and puzzling of Night Monkey vocal patterns.

Gulps are very common, probably even more so on the average than Gruff Grunts. They were uttered by all the adult individuals studied during the present investigation.

A single Gulp is usually moderately loud and always rather "liquid" sounding, rather like a human belch. Sketches of the sound spectrograms of two typical Gulps are shown in figure 11. The mouth remains apparently closed during the utterance of all or most Gulps; but every Gulp is accompanied by a brief swelling of the throat (to all appearances the same as the inflation accompanying Gruff Grunts described above).

Gulps are usually uttered in series. A single uninterrupted series seldom includes more than five notes, and series of only two or three notes are quite common; but series are often repeated rapidly one right after the other, with only brief pauses between successive series.

An overwhelming majority of all the Gulps heard were uttered by individuals engaged in vigorous locomotory activities. They were uttered during most periods of really active running and leaping in almost all social circumstances.

One type of performance was particularly remarkable. As noted above, Night Monkeys generally are most active just after sunset and just before dawn. During the predawn periods, the captive animals kept in large cages on Barro Colorado Island usually ran and leapt around their cages rapidly and almost continuously for a half hour or more. Single individuals alone in their cages, mated individuals in cages with their mates, and individuals kept together in larger groups, all tended to behave in much the same way at such times. They seldom interrupted their running and leaping to feed or drink or groom themselves, and the individuals that had companions in their cages seldom performed unmistakable hostile or sexual patterns. They

all tended to utter many Gulps during such periods, but relatively few or no other notes (except Sneeze-grunts—see below). Most of the wild Night Monkeys on Barro Colorado Island also uttered many Gulps and relatively few obviously hostile or sexual calls just before dawn.



FIG. 11.—Two Gulps, uttered by an adult.

Based upon a spectrogram by a "Missilyzer."

It will be seen that these notes are rather similar to the Sneeze-grunt shown in figure 9. There are, however, a few definite differences. The Sneeze-grunt has a range of frequencies between 0 and approximately 650 cycles per second (c.p.s.), all starting at exactly the same time and having predominant amplitudes and longer signals around 100 c.p.s. and 260 c.p.s. The Gulps begin with high frequencies around 850 c.p.s., and drop rapidly in frequency to fairly equal amplitude signals between approximately 240 and 600 c.p.s.

The causation and function(s) of this intense (and often apparently "purposeless") activity were difficult to identify. It is possible that Night Monkeys, like some other mammals that normally range over large areas (*e.g.*, many canids—see Lorenz, 1952), have a strong "internal" tendency to perform locomotory movements, a tendency expressed by overt activity even when the other immediate needs of the animals (*e.g.*, food, water, and sex) can be fully satisfied without moving about very much.

If so, many or all Gulps may be expressions of the same "independent" locomotory tendency. They may be produced when the loco-

motory tendency is too strong to be completely expressed by running and leaping movements alone.

There are other indications, however, that some or all of the Gulps may be at least partly hostile. Although most overt escape and simple alarm patterns are silent (see page 13), Gulps are often uttered before and/or after such reactions. Very occasionally, Gulps are uttered by individuals that are not running or leaping at the time. One captive individual on Barro Colorado, for instance, uttered a particularly loud and rapid series of Gulps while sitting, frozen, in a crouch posture immediately after overt escape. It is also my impression that the wild individuals in the forest tended to utter relatively few Gulps when they were apparently unaware of being observed. The frequency of their Gulps sometimes increased greatly at the instant they seemed to become aware of the presence of an observer—even when their other activities continued unchanged.

It is possible, therefore, that some or all of the Gulps may be produced by a combination of locomotory and escape tendencies, usually when the latter is relatively and/or actually weak.

The Gulps may exemplify a complex evolutionary change.

Although they are probably partly hostile in motivation, they do not appear to be hostile in function. (They certainly do not function as warning signals. I have never seen a Night Monkey respond to the sounds of Gulps by performing overt escape.) They may well function as "contact notes." They may help to keep mated individuals and members of the same family group together under natural conditions. The utterance of Gulps by one individual should enable its companions to tell exactly where it is (especially as Gulps are very penetrating, even when not very loud).

No other species of platyrrhine monkey with which I am familiar utters similar notes with similar frequency in similar situations.² This would suggest that Gulps, as adult contact notes, are highly specialized. If so, they probably have been derived from some purely hostile Grunt pattern. (They are similar to Gruff Grunts in some aspects of

² Adult individuals of some other species, *e.g.*, some tamarins, may utter "lost" notes or calls when completely isolated; but such notes or calls are seldom or never uttered by individuals moving about near other individuals of the same species in the same way as the Gulps of Night Monkeys.

Adult howler monkeys of the species *Alouatta palliata* may utter some notes which help to maintain contact between the members of a band (Carpenter, 1934, and Collias and Southwick, *op. cit.*); but such notes seem to be uttered relatively much less frequently than the Gulps of Night Monkeys, and may be produced by rather different motivation.

form—see accompanying figures—and gruntlike patterns are widespread among many species of New World monkeys.)

It should be mentioned, in this connection, that the Gulps of Night Monkeys are uttered in almost exactly the same social circumstances as the contact notes of some species of Panamanian birds, and that the latter seem to have had a similar evolutionary history, also being derived from purely hostile patterns (Moynihan, 1963a).

The development of Gulps as contact notes may be another adaptation to nocturnal habits. Night Monkeys probably cannot keep in touch with their companions by sight as easily as can other platyrrhines.

(While recording the sounds of captive Night Monkeys on Barro Colorado Island, a few short and single "twanging" noises were heard, through the earphones of the recording machine. Unfortunately, these noises were always heard at times when the animals were not under observation. They probably were not mechanical in origin [at least, I could not find any object in the animals' cage which looked as if it could be used to produce such noises] ; but nothing similar was heard in other circumstances. To my ears, the noises sounded as if they might be Gulps uttered in *very* close proximity to the microphone. This theory does not, however, seem to be supported by sound spectrograms [see figure 12]. The significance of these noises remains problematical.)

One captive Night Monkey at Iquitos uttered series of gulping notes which had a distinctive hooting quality (rather as if "ooo" sounds were superimposed upon the ordinary Gulps of Barro Colorado animals). These notes were uttered while the animal was moving about its cage in a perfectly normal manner. They may have been a characteristic pattern of the local population of Night Monkeys, or an individual peculiarity, or (possibly) intermediates between typical Gulps and typical Hoots.

Both the wild and captive animals on Barro Colorado Island were heard to utter Sneeze-grunts.

A single Sneeze-grunt sounded like a single sneeze superimposed upon a single, loud, typical Gruff Grunt. The sound was always sharp and abrupt. Most Sneeze-grunts were also at least slightly nasal in tone (each note might be transcribed by something like "Aaanh"). Figure 9 includes a sketch of a sound spectrogram of a more or less typical Sneeze-grunt.

Sneeze-grunts were usually uttered singly. Sometimes two were uttered together in quick succession ; but they never occurred in longer series like Gulps and Gruff Grunts.

They were uttered with the mouth closed or nearly closed, and

apparently were not accompanied by conspicuous inflation of the throat region.

They were almost always much less common than Gulps, but were uttered in the same types of situations, usually by individuals moving about very rapidly and energetically. They were frequently uttered in close temporal association with Gulps. In such cases, the most common arrangement was two or three Gulps, followed by a single Sneeze-



FIG. 12.—A single "twanging" noise heard while recording adults.

Based upon a spectrogram by a "Vibralyzer."

grunt, followed by two or three more Gulps, followed by another Sneeze-grunt, etc.

Sneeze-grunts also were uttered quite frequently in close association with Moans and Trill patterns. In such cases, the notes were usually arranged in "doublets" of one note of each type: A single Moan followed immediately by a single Sneeze-grunt, or a single Sneeze-grunt followed immediately by a single Low or High Trill, or (most frequently) a single Sneeze-grunt followed immediately by a single Moan. These arrangements were stereotyped enough to suggest that they may have become partly ritualized *per se*.

It seems probable that the Sneeze-grunts were produced by some combination of locomotory and escape tendencies similar to that producing Gulps. It was noticeable, however, that Sneeze-grunts were most likely to be uttered just before or just as an individual made a long leap, while Gulps were relatively more frequently associated with shorter leaps and running movements. Similarly, when wild Night Monkeys were encountered in the forest, they sometimes uttered Gulps when approached in the dark, switched to Sneeze-grunts when a light was put on them, and then retreated in overt escape. Such facts would suggest that the Sneeze-grunts may have been produced when the escape tendency was stronger than in all or most Gulps.

The Sneeze-grunt is the only Night Monkey pattern similar to the ordinary Warning Notes of many other New World monkeys in form. It resembles the latter in being loud, sharp, and usually single. It may well be phylogenetically related to the Warning Notes of other species, and may have functioned in the same way in the ancestors of the Night Monkey, alerting other individuals of the same species to possible danger in the environment and inducing them to escape. It does not, however, seem to function in this way at the present time. Its signal effect is obscure at present; but it may be another contact note like the Gulps.

DISCUSSION

The preceding list includes almost all the typical vocal patterns of adult Night Monkeys.³ It may be useful, therefore, to add some general comments about their vocal repertory as a whole.

Adult Night Monkeys do utter vocalizations which are more or less obviously intermediate between otherwise distinct types of notes. Some of these intermediates have been mentioned above; others include intermediates between Moans and Gruff Grunts, between Gruff Grunts and Gulps, and between Sneeze-grunts and Gruff Grunts.

Although some of these intermediate vocalizations are uttered with appreciable actual frequency, they seem to be comparatively rare, and are uttered relatively less frequently than intermediate notes in the repertories of adults of some related species, *e.g.*, species of *Saimiri*,

³ Some brief experiments with an ultrasound detector would indicate that neither the adults nor an infant kept in captivity on Barro Colorado uttered any calls or notes completely inaudible to the human ear. In this respect, Night Monkeys seem to differ from at least one other species of New World primate, the Pygmy Marmoset (*Cebuella pygmaea*).

Cebus, and *Ateles*. In these latter species, all or most of the major adult vocal patterns seem to intergrade with one another through nearly continuous series of common intermediate notes.

Such differences in organization of the vocal repertory presumably are correlated with different ways of functioning.

When an adult of a *Cebus* species is motivated by three or four different tendencies (*e.g.*, attack, escape, sex, and gregariousness), it may be able to express *all* the tendencies simultaneously by uttering a single ambivalent vocal pattern, more or less perfectly intermediate between the patterns which would be produced by each one of the tendencies (or pair of tendencies) if activated alone. A signal of this type must contain a relatively large amount of information. This in itself must be advantageous. But such signals may have disadvantages as well. It may be difficult for the receiver of a signal of this type to perceive or "decipher" all the information contained in the signal. Complex signals are probably more easy to misunderstand than simple signals containing less information. In these adult monkey repertoires, it is also probable that the frequency of intermediate notes reduces the contrast between different signals. These features may induce momentary confusion in the individual(s) toward which the signals are directed. Even when confusion is avoided, they must tend to reduce the speed of the response to the signals. This is probably very disadvantageous. There is evidence that selection always or nearly always tends to favor increased rapidity of social responses (Moynihan, 1963b).

An adult Night Monkey motivated by a complex combination of tendencies usually does not utter intermediate notes, but rather a series of different types of notes, each one of which expresses only one or two of the tendencies. Thus, for instance, a wild adult surprised by a disturbing stimulus may utter a rapid "jumble" of Gruff Grunts, Moans, Gulps, Low Trills, and Sneeze-grunts, *not* a single vocal pattern expressing the complete combination of attack, escape, locomotory, and (possibly) other tendencies by which it is motivated. This sort of message may be able to convey as much information as a single note expressing all the tendencies simultaneously, if the arrangement of the different notes is not random and if the receiver's reaction to the first note does not interfere with its reactions to the later notes; but it is certainly produced with greater physical effort and, more important, more slowly. The principal advantage of this sort of message presumably is that each one of its constituent notes, being an expression of only one or two tendencies, is a comparatively simple signal and, therefore, difficult to misunderstand.

The principal differences between these two types of platyrrhine vocal repertoires may be summarized as follows. In one type, the information is coded very rapidly in an economical form but may be difficult to read, or difficult to read rapidly. In the other type, the information is coded less rapidly and efficiently but can be read more easily and/or more rapidly.

The relative importance of the advantages and disadvantages inherent in each type of repertory may be different depending on the circumstances and environments. The type of repertory possessed by adult Night Monkeys may be another (partly indirect) adaptation to nocturnality.

Adults of *Saimiri*, *Cebus*, and *Ateles* can avoid some of the disadvantages inherent in their type of vocal repertory by combining the information received from auditory signals with information derived by another method of perception. They are all thoroughly diurnal, and must usually be able to see other animals and objects in their environment quite clearly at considerable distances. As noted above, both *Cebus* and *Ateles* species have a wide variety of facial expressions which function as signals. They also have many other display postures and movements involving other parts of the body; and so does *Saimiri*. Any adult individual of these species hearing calls or notes from another individual of the same species usually will perceive visual signals and/or receive visual clues from the physical environment at the same time. These visual aids should enable the individual to grasp the significance of any vocal pattern, even when the latter is difficult to decipher or ambiguous in itself.

As adult Night Monkeys usually receive less visual information (because they are nocturnal and frequently become separated from one another and have fewer visual displays), they are more dependent upon auditory signals and more likely to misinterpret any possibly ambiguous vocal patterns. It must be absolutely essential for them to have a system of vocal patterns which are easily and immediately comprehensible, whatever the inevitable disadvantages of such a system.

It is probably significant, in this connection, that infant and juvenile Night Monkeys utter relatively more intermediate notes than do adults (see below). The vocal signals of infants to their parents may be supplemented by tactile stimuli, as the infants are always carried by their parents. Even when no longer carried, juveniles may be able to provide important supplemental visual information because they tend to remain very close to their parents.

To my knowledge, the only Old World monkey in which this aspect

of behavior has been studied is the Rhesus, *Macaca mulatta*. According to Rowell and Hinde (1962), the vocal patterns of this species also intergrade through frequent intermediates. Rhesus Monkeys are diurnal, and have many visual displays, including many different facial expressions (Hinde and Rowell, 1962).

These facts would suggest that there may be a general rule among monkeys that species or classes of individuals largely dependent upon auditory signals for the regulation of their social behavior tend to have discrete, sharply delimited vocal patterns, while species or classes of individuals less dependent upon auditory signals tend to have intergrading vocal patterns.

The major vocal patterns of adult Night Monkeys not only are discrete but also sound quite different from one another to human ears. This is true of patterns that look somewhat similar in sound spectrograms, *e.g.*, Gulps and Sneeze-grunts, as well as of patterns that look very different. There is every reason to suppose that the contrasts between different types of patterns are equally obvious to the Night Monkeys themselves. It is quite evident from their behavior that the hearing of Night Monkeys is at least as good as that of human beings.

Contrasts in sound may facilitate rapidity of comprehension when messages are composed of many notes of different types.

The probable importance of this feature is emphasized by the fact that all the associations between different types of notes that are particularly common and/or seem to be ritualized *per se* are associations between notes that contrast with one another in a particularly striking manner. In some cases, *e.g.*, Gulps and Sneeze-grunts, the associated notes seem to serve similar functions. In other cases, *e.g.* Sneeze-grunts and Moans, they seem to serve quite different functions. Associations between notes that are somewhat less conspicuously contrasting in sound, *e.g.*, Moans and Low Trills, seem to be less frequent and/or less close.

It is conceivable that information conveyed by contrasting stimuli may tend to produce stronger reactions (*i.e.*, may appear to be more "emphatic" to the receiver) than the same information conveyed by stimuli with less contrast; but this would be very difficult to prove.

In spite of the obvious differences between the hostile vocal patterns of adult Night Monkeys, there are some morphological resemblances between many or most of them. This is certainly true of Gruff Grunts, Resonant Grunts, and Sneeze-grunts. A few similarities between Gulps and both Gruff Grunts and Sneeze-grunts have already been mentioned. It may be convenient to refer to all these patterns, together,

as the "Grunt Complex." The low-pitched Moans and Low Trills may be related. It is possible that all the patterns of this complex have been derived, in whole or in part, from a single pattern or a single group of completely intergrading patterns (perhaps comparable to the "basic agonistic sound" of the Rhesus Monkey described by Rowell, 1962) in the course of evolution.

The hostile vocalizations of adult Night Monkeys seem to be produced when motivational conflict is stronger, *i.e.*, when incompatible tendencies are more nearly equal in strength, than when many or most of the nonvocal hostile displays are produced. A similar arrangement occurs in some species of birds (see, for instance, Moynihan, 1962b). It may be characteristic of most higher vertebrates.

Some other aspects of the vocal behavior of Night Monkeys will be discussed below, in connection with the Hoot and Squeak patterns.

SOCIAL SNIFFING

This is the most common of the "greeting" patterns. In captivity (at least), it is almost always performed whenever any two previously unacquainted individuals meet one another for the first time, and it also occurs in certain other social circumstances.

It may be initiated by either one of the individuals involved, or by both simultaneously. A sniffing animal simply approaches another, stretches its neck forward a little, and smells the other, usually for at least several seconds. When sniffing is initiated by one individual, the individual being smelled remains motionless at first, but usually responds by sniffing in return if the first individual continues long enough. Sometimes two individuals will sniff one another alternately. More often their sniffing overlaps in time, even when they do not begin simultaneously.

Most sniffing—both mutual sniffing and sniffing by only one individual—begins "nose to nose." An individual usually starts by bringing its face as close as possible to the face of its "partner" in the performance. It also may sniff into the armpit or under the arm and/or at the perineal region of its partner. This is relatively (if not actually) rare as an initial reaction, but it is very common immediately after nose-to-nose sniffing. Occasionally, two individuals will sniff at one another's perineal regions simultaneously. This is done less frequently by Night Monkeys than by some tamarins (for which it is the usual form of social sniffing).

It seems likely that this behavior is guided by, or orientated toward, special scent glands. The skin glands of Night Monkeys have been

described by Hill, Appleyard, and Auber (1959) and Hanson and Montagna (1962). Apocrine glands are largest in the face and genital areas. Lateral to the alae of the nose they are intermingled with large sebaceous glands. There are also larger and more specialized glandular organs in the sternal region and at the base of the tail. It is possible that individuals which appear to be sniffing in the armpits of their "partners" are really trying to get at their sternal organs.

When complete strangers are introduced to one another, they may repeat social sniffing whenever they come close to one another during the first few hours (or nights) after the introduction. This behavior may disappear, gradually, as the animals become familiar with one another. Only in the case of males and females that become mated to one another does social sniffing remain frequent in certain situations. Mates often perform social sniffing immediately before copulation and related patterns (see below).

Social sniffing was performed by all the captive animals observed, at Washington and Iquitos as well as on Barro Colorado Island. It seemed to be performed with approximately equal frequency by all individuals in similar circumstances in captivity.

Very tame, hand-reared individuals in captivity on Barro Colorado Island sniffed at human beings occasionally, especially if they were familiar with the person involved but had not been visited by him or her for some time.

Although social sniffing may be followed by high-intensity hostile behavior as well as (or instead of) copulatory reactions and may be accompanied by a variety of vocalizations, such as Trills and Squeaks, it is probably purely investigatory in itself. The first part (at least) of social sniffing seems to be essentially the same as the sniffing of food described above.

SEXUAL BEHAVIOR AND ASSOCIATED OR RELATED PATTERNS

The term "sexual behavior" will be used in a broad and general sense throughout the following pages to include all behavior patterns characteristically directed by adult individuals of one sex toward adults of the other sex, or performed by adults of one sex in the presence of the other.

The causal factors responsible for the performance of sexual activities by Night Monkeys are particularly difficult to identify, even tentatively, for several reasons.

In many species of higher vertebrates, all or most sexual activities

seem to be produced by two main types of motivation: A pairing tendency, which is satisfied by the presence of a mate, and a copulatory tendency, which is satisfied by the performance of a successful copulation (or ejaculation in the case of male). Night Monkeys may have the same two tendencies; but this could not be confirmed, during the present study, because of the practical difficulty of observing the usual long-term sequence of sexual reactions under natural conditions.

In many other species of New World monkeys, it is possible to distinguish between the sexual tendencies and a gregarious tendency, which is satisfied by association with other adult individuals of the same species irrespective of sex. This cannot be done in the case of the Night Monkey, simply because adults of this species do not usually associate with any other adults of the same species except their own mates. It is conceivable, however, that the complex of factors producing the sexual behavior of Night Monkeys includes components homologous with the gregarious tendencies as well as the strictly sexual tendencies of related species.

HOOTS

Both wild and captive adult Night Monkeys on Barro Colorado Island uttered Hoots. So did a subadult individual, who seemed to be behaving in an essentially adult manner, at Iquitos. Among the captive individuals on Barro Colorado Island, Hoots were uttered by both males and females. The individual Hoots of all these animals sounded similar or even identical (apart from some variation in loudness) to my ears.

They were low-pitched, moderately prolonged, and at least moderately loud. Each individual Hoot sounded to me like a single note. I seem to have been misled, however. A sketch of what sounded to me like three Hoots is shown in figure 13. It will be seen from this that each one of the apparently unitary Hoots was actually compound, composed of one or two relatively long sounds, followed by two to five short sounds, with only very brief intervals between them.

In spite of this discrepancy, it will be convenient to refer to each hooting pattern that sounded to me like a single note as a "Hoot" or "a note." The briefer sounds making up a Hoot, in this sense, will be referred to as "components of a Hoot." Using these terms, it can be said that the intervals between the components of a Hoot were always *much* shorter than the intervals between successive Hoots or between a Hoot and any other type of call or note.

(The Hoots sketched in figure 13 were uttered by an adult female. Unfortunately, these were the only Hoots uttered by an adult of

which it was possible to make spectrograms. They seem to have been somewhat different from the Hoots of a young male sketched in figure 20. I think that the differences between the Hoots of these two individuals were due to the difference in their age, not their sex.)

The adult Night Monkeys on Barro Colorado Island uttered Hoots singly and in short series of two, three, and four notes. Two was the most common number. The Iquitos animal apparently always uttered Hoots in series of three or four.

The postures and movements accompanying Hoots were observed only in captive individuals. The Barro Colorado adults uttered their Hoots while sitting in a perfectly normal unritualized posture, hind

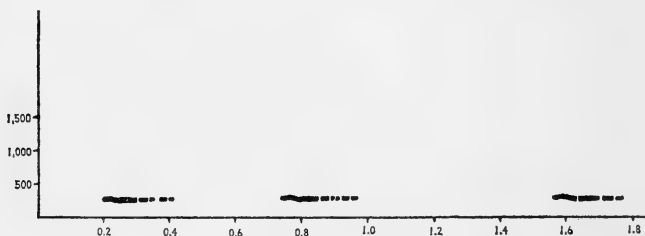


FIG. 13.—Three Hoots, uttered by an adult female.

Based upon a spectrogram by a "Sona-graph."

The harmonics accompanying these notes are not shown.

limbs flexed, back slightly curved (as in all sitting postures), and hands firmly grasping the perch. They usually looked more or less straight forward throughout their performances. The mouth was opened slightly as each Hoot was uttered, and apparently closed between the successive notes of a series. The throat and upper breast were inflated with each note, and subsided between notes. The Iquitos animal sat in a similar posture but looked almost straight downward throughout its performances. This may have been a low intensity indication of a head-down pattern (the animal had not been in its cage very long, and it may have been somewhat shy). A single adult female on Barro Colorado looked downward briefly (and perhaps lowered her whole head) as she uttered Hoots in otherwise typical series, but she always looked up (and perhaps raised her head) between each note of a series.

These captive individuals were always (with one exception—see page 51) alone in their cages, or at least the only individuals of their

own species in their cages, at the times that they uttered Hoots. Any adult that had been Hooting regularly every night always (again with the same single exception) stopped Hooting as soon as another Night Monkey was put in the same cage. The Hoots stopped irrespective of whether the animals fought with one another and/or performed copulatory reactions or did neither. (I might add that Hoots were not uttered during disputes between individuals in different cages, even "long-range" hostile reactions between individuals in cages quite far apart from one another.)

As far as I could tell, all the wild individuals heard to utter Hoots were also alone at the time.

These facts would suggest that the Hoots of adult individuals are produced when a gregarious and/or a pairing tendency is thwarted by the absence of a suitable companion.

Although I was never able to observe responses to Hoots in the forest on Barro Colorado Island, it seems likely that their primary function, when uttered by unmated adults under natural conditions, is to attract potential mates. If so, they are essentially similar to certain types of bird vocalizations which have been called "song." (Another resemblance to most "song" is that an individual uttering Hoots, *i.e.*, "wanting" a companion, apparently always remains stationary, instead of going in active search of a companion. It has already been mentioned that the captive individuals sat during their Hoots. Wild individuals frequently moved from tree to tree between series of Hoots, but they were never heard to move during the utterance itself.)

The single case of Hooting by an adult in the same cage with another individual of the same species, cited above, occurred immediately after a male and a female had been brought together again after a long separation. They were probably mated before, but may have become incompatible during the period of separation. The female uttered many Hoots during the first few nights after the animals were brought together again; but all her Hoots were unusually soft and probably low intensity.

The Hoots of Night Monkeys sound very much like some notes of owls. There is, in fact, one species of owl on Barro Colorado Island which utters hooting notes that are almost identical (to human ears) with those of Night Monkeys (except for the fact that they are always or almost always uttered singly). It is possible that notes of this type have acoustic properties which are particularly advantageous in tropical forests at night.

It seems probable that the pitch, at least, of almost all the char-

acteristic vocal patterns of adult Night Monkeys is a specialized adaptation to such conditions. Apart from the Screams (and the Squeaks, if they are a "normal" pattern of adults—see page 58), all the adult calls and notes are comparatively low in pitch. The vocal repertory of adult Night Monkeys is lower, on the average, than the adult repertory of any other New World primate with which I am familiar, except the howlers of the genus *Alouatta*. It is certainly much lower than the repertory of any other New World monkey of comparable size. All other factors being equal, a low-pitched sound will carry farther than a high-pitched sound of equal energy value at the starting point. In all circumstances, the energy of high-pitched sounds will be used up more rapidly than that of low-pitched sounds. Another property of low-pitched sounds may be particularly significant in a forested environment. The relatively long sound waves of low-frequency noises will be less affected, *i.e.*, deflected or scattered, by obstructions such as twigs and branches than the shorter waves of high-pitched sounds. Low-pitched sounds may be particularly useful to adult Night Monkeys because they are largely dependent upon auditory signals for long-distance communication.

It must be significant, in this connection, that the high-pitched Screams seem to be the only purely hostile vocalizations of adults that are always short-range signals. Similarly, the only Squeaks that may be a regular part of adult behavior are uttered only when two individuals are in actual physical contact with, or in very close proximity to, one another (see below).

RUBBING

The only individuals observed to perform this pattern were the captive adults on Barro Colorado Island.

In the most complete and vigorous Rubbing performances, an individual would flex its hind legs, press its perineal region against a branch, and then rub the whole region against the branch with rapid side-to-side movements. Generally there were two or three movements in each direction. The tail was usually lifted at the same time, and frequently twitched from side to side. The gland at the base of the tail may have brushed against the branch during these movements, but I was never able to make sure of this.

Low-intensity Rubbing consisted of nothing more than one or two sideways "swipes" at a branch, sometimes very poorly orientated.

All Rubbing was usually silent.

Some individuals had favorite Rubbing sites—particular spots

where they performed Rubbing much more frequently than elsewhere. All or most of these sites were places where there was a slightly projecting irregularity on the surface of a branch, or even the stump of a projecting twig.

As an intraspecific reaction, Rubbing was performed almost exclusively during encounters between males and females, usually encounters in which either one or both individuals also performed overt (and often high-intensity) hostile and copulatory patterns. Low-intensity Rubbing might be performed by either one or both individuals during such encounters; but complete and vigorous Rubbing generally was performed only by females. Most male Night Monkeys tend to be slightly dominant over females. It may be significant, therefore, that the only male observed to perform high-intensity Rubbing during an intraspecific encounter was obviously subordinate to the female with which he was associated at the time. He would seem to have been playing a feminine role. Although usually subordinate, the females that performed high-intensity Rubbing were not very frightened. They usually did their Rubbing as they approached males, to initiate either overt hostility or precopulatory behavior (or both).

Some very tame individuals performed low-intensity Rubbing movements when approached by human beings. A moderately tame individual (almost certainly a male), in a cage with its mate and young, repeatedly performed vigorous and complete Rubbing after being approached by a human being, as the latter walked away.

These facts would suggest that Rubbing is usually produced by some combination of hostile and sexual tendencies. (Some other "friendly" social tendency may take the place of sex in some circumstances.) Possibly some territorial motivation is also involved. (It is not yet clear how the motivation of Rubbing differs from that of Moans or Low Trills. There is not enough evidence to permit a choice among the several possibilities that come to mind.)

Rubbing is probably related, phylogenetically, to the "territory marking" patterns of many other mammals (which are very similar in form). Night Monkeys may spread some odoriferous substance on the branches that they rub against. But I have never seen a Night Monkey smell or sniff at the Rubbing site of another individual in an unusually attentive manner.

The Rubbing by the individual with its mate and young appeared to be a "triumph ceremony," proclaiming the successful defense of its territory, in much the same way as some Resonant Grunt performances.

Hill (1960) says that captive Night Monkeys may moisten the palms of their hands and the soles of their feet with urine, and he compares this habit to the similar pattern of nocturnal Lorisoidea which has been interpreted as a method of marking territory. I never saw anything like this in any of the Night Monkeys that I studied. It may be confined to other populations of the species and/or a result of special conditions in captivity.

I might add, in this connection, that I have never seen such behavior performed by Tufted Capuchins (*Cebus apella*) kept in captivity on Barro Colorado or in the Zoo at Lima, Peru, although Nolte (1958) reports it as common among some individuals of the same species kept in captivity in Rio de Janeiro. This sort of behavior may be extremely variable among Platyrrhini.

COPULATIONS, ALLOGROOMING, AND ASSOCIATED PATTERNS

Like many other New World primates, Night Monkeys seem to perform overt copulatory reactions rather infrequently under natural conditions. I never saw copulations by the wild individuals on Barro Colorado Island. Copulations are also at least relatively rare among captive individuals. The only captives observed to perform copulatory reactions or closely related patterns were the ones on Barro Colorado Island. Even here, the copulatory reactions of mated individuals kept together continuously were not only rather infrequent but also rapid, brief, and inconspicuous. The only really elaborate and conspicuous sequences of copulatory patterns were performed by males and females coming together for the first time or rejoining one another after being separated and kept in isolation for several weeks or months.

The most simple forms of apparently successful copulations are simple indeed. In such cases, the male and female tend to approach one another silently. The male usually sniffs at the female's genital or perineal region, either immediately or after sniffing at her face. The female may sniff at his perineal region while he sniffs at hers. He then mounts her from the rear, clasps her around the upper part of her body with his arms, and maneuvers his body into a position from which he can insert his penis into her vagina under her tail (she may lift her tail, or shift it sideways, as he does so, but this movement is always very slight). After insertion, the male usually makes three or four pelvic thrusts. Ejaculation apparently occurs only during the last thrust, which sometimes is sustained relatively long. The whole lower part of the male's body may quiver visibly during this last thrust. The male then dismounts. Sometimes his dismounting seems to be accelerated by the female turning her head to look at him.

Apart from this, the female seems to remain essentially passive throughout the whole performance. Both individuals generally are silent throughout. The whole performance seldom or never takes more than a couple of minutes. Sometimes it is much briefer. There is no regular postcopulatory display; although it is not uncommon to see a female sniff at the male's perineal region, briefly, immediately after he dismounts.

Simple and rapid copulations of this type seem to be performed only when both the male and female are highly motivated and thoroughly familiar with one another.

A pattern frequently associated with less simple copulation attempts is Allogrooming. One of the individuals grooms the other, or they groom one another mutually. When only one individual performs Allogrooming, it may be either the male or the female. It is usually the male when the Allogrooming occurs in very close association with apparently successful copulation attempts. The form of the Allogrooming movements seems to be the same in both sexes.

One individual wishing to groom another generally begins by sniffing. The "groomer" usually sniffs most attentively at the sides, armpits, or perineal region of the "groomee." The actual grooming follows immediately after the sniffing. It is accomplished by use of both hands and teeth. The use of the teeth seems to be most important in Allogrooming (unlike autogrooming). The grooming individual nibbles at the fur and/or skin of the individual being groomed, presumably separating matted hairs, removing dead hairs and patches of dead sloughed skin, and also any small arthropods that may be present (both ticks and chiggers are common, at times, on Barro Colorado). The hands are used both to "curry" or comb the fur of the individual being groomed and, even more frequently, to separate the fur so that the grooming individual can get at the base of the hairs and the skin with its teeth. During some Allogrooming, the groomer uses its hands to push or pull the groomee into a position or posture to facilitate the grooming.

The groomer may groom any and all parts of the groomee, in almost any sequence; but it usually devotes most of its attention to the sides, back, crown and back of the head. The two animals generally sit side by side during Allogrooming, facing in the same or opposite directions, and the groomer reaches the groomee from the side and/or the rear (see figure 14).

Allogrooming may lead to mounting. This "grooming mounting" may intergrade with the type of mounting that occurs during copulations, and intermediate performances are common, but in its typical

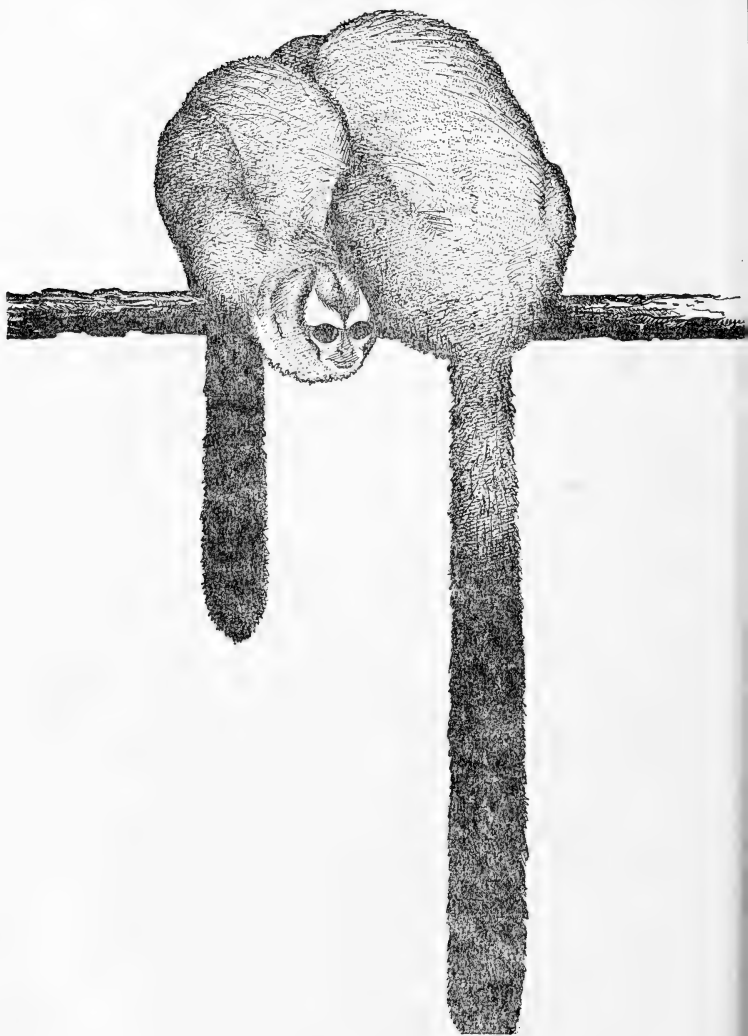


FIG. 14.—Positions and postures sometimes assumed by mated individuals during Allogrooming.

The individual on the right is grooming the individual on the left. The lowering of the front part of the body by the latter is probably a balancing reaction, *not* an indication of a head-down posture.

form it is quite distinct. It occurs when the groomer wants to groom areas on the far side of the groomee. In its attempt to get at these areas, the groomer may climb up on the back of the groomee. It usually climbs up from the side, not from the rear as in the case of a male mounting a female during a typical copulation attempt. A grooming individual also tends to keep its head pressed down into the fur of the groomee. (A male generally does not lower his head as much during copulation). The only individuals observed to perform grooming mountings were males; but this may have been largely due to the fact that most of the females observed were slightly subordinate to their males and somewhat reluctant to handle them roughly (there is no obvious reason why females should not be able to perform such mountings in suitable circumstances).

If the individual being groomed does not object to the process (and rough or awkward Allogrooming may provoke disputes—see below), it remains passive, sitting quietly. Only rarely does it shift position voluntarily to present particular areas that it wants to have groomed.

Night Monkeys do not seem to have any special “soliciting” posture to invite (initiate) either copulation or Allogrooming (unless sitting quietly by the side of another individual can be considered such).

Some Allogrooming performances are quite silent. Others are accompanied by Squeaks and/or a variety of wholly or partly hostile notes (see below). Hostile notes are relatively very rare except during the obviously “unsuccessful” performances which break up in open disputes.

Allogrooming may occur immediately before and/or after both successful and unsuccessful copulation attempts. It may also occur apart from overt copulation attempts, but only relatively rarely. Almost all the individuals observed to perform such grooming were known to be in reproductive “mood,” copulating with the individuals they groomed on succeeding and/or preceding nights, even if not always immediately before or after the actual grooming.

These facts would suggest that the copulatory tendency may be at least one of the causal factors producing Allogrooming in all circumstances.

The detailed relations or interactions between Allogrooming and overt copulatory movements are rather complex. In spite of their frequent association, and their apparent similarity in motivation, the two types of behavior seem to be mutually exclusive, to some extent, on a short-term basis. Allogrooming appears to serve as a partial “substitute” for copulation. It is very common to see a male groom

a female *briefly* before mounting and performing an apparently successful copulation; but he will almost certainly *not* copulate successfully, or at least will not copulate successfully immediately after the Allogrooming, if he grooms her vigorously for more than a few seconds.

This would suggest that the performance of prolonged Allogrooming tends to "consume" an appreciable amount of copulatory motivation, *i.e.*, raises the releasing threshold of overt copulatory behavior in at least many circumstances.

Allogrooming may have several functions. Its successful performance may help to reduce the actual or potential hostility between male and female. The close physical contact involved may also provide some direct sexual stimulation.

Either one or both of these effects may be very rapid. They may be more rapid but less long sustained and/or have less potential strength than the effect of raising the threshold for copulatory behavior. If there are such differences in speed, and possibly strength, between the contradictory effects of Allogrooming, this would explain why successful copulations frequently follow brief grooming and rarely follow prolonged grooming.

Repeated Allogrooming may also have the relatively very long-term effect of strengthening the pair bonds between mates.

If the Allogrooming of Night Monkeys does function in these different ways, it is basically similar to many "precopulatory" patterns of other species, *e.g.*, the Allogrooming of many other mammals and the Food-begging and Allopreening of many birds.

The penis of a male Night Monkey may be erected before he mounts during copulation, but it is not "shown off" to the female. This behavior pattern does not seem to be a ritualized display like the penile erection of Squirrel Monkeys, *Saimiri*, described by Ploog and MacLean (1963).

The only other patterns which must be considered in connection with the sexual behavior of Night Monkeys are Squeak notes. These seem to be typical of young animals and infants, but are uttered also by adults in certain circumstances.

Many of the Squeaks uttered by adults may be reversions to, or persistent remnants of, juvenile behavior; and may be produced by some or all of the same wide range of causes as the Squeaks of juveniles (see below). Squeaks are certainly uttered more frequently by adult individuals that have been raised in complete or partial isolation from other individuals of their own species than by adults raised in the wild under natural conditions; and the retention of juvenile

patterns by adults is the sort of phenomenon which might be expected to be produced by the abnormal circumstances of captivity. (If nothing else, young animals raised in captivity tend to regard the human beings that take care of them as their parents, and often retain this attitude after reaching maturity, long after they would have become independent of, or separated from, their parents in the wild.)

Other Squeaks uttered by adults may have a different significance. Many of the captive adults on Barro Colorado Island uttered frequent Squeaks during sexual reactions. This occurred often enough to suggest that Squeaks may be a normal part of the adult repertory, a normal accompaniment of sexual behavior even if not of any other adult activity.

Squeaks were uttered by both adult males and females. They were uttered most frequently by individuals approaching their mates, and just beginning to perform Allogrooming, but were relatively much less frequent during the later stages (when Allogrooming was in full swing and most vigorous). Squeaks also were relatively rare during copulations and overt disputes between mates.

As far as I could tell by ear, all the Squeaks uttered by adults were similar to, or identical with, the "pure" Squeaks of juveniles in form.

The function(s) of adult Squeaks in sexual situations were obscure. They did not seem to produce any overt, positive, response in the individuals toward which they were directed. They may, conceivably, have functioned as some sort of appeasement pattern. One might expect that any behavior pattern that is performed most frequently by infants and juveniles would tend to reduce hostility (especially aggressiveness) in any adult toward which it is directed, even when it is performed by another adult.

EXAMPLES

Some of the different sequences and combinations of Allogrooming, copulatory, hostile, and other patterns during different types of encounters between males and females may be illustrated by extracts from my notes made at the times of observation.

The first is an example of the behavior of experienced males and females.

February 4, 1962. Z male and X female. These two animals are mates. They were separated several days ago. The male has been kept in the cage in which the pair lived previously. The female has been kept in another cage (out of sight and hearing of the male) by herself.

7:40 p.m. Female put back in cage with male. Male is in sleeping box at the

time. Female rushes straight toward him. He comes out of box. The two animals sniff at one another's perineal regions. Then the male mounts the female, from the rear. No hesitation or awkwardness. Copulation. Apparently successful. Lasts at least 20 seconds. Then the male dismounts. No postcopulatory display. Male walks away, female follows. She utters two Low Trills as she does so.

7:44. The two animals sniff one another's perineal regions again. And again. Silent. No Allogrooming or attempts to mount. Then sit side by side. One or both utter(s) a few Squeaks. Then male does begin to groom female. From side. Then mounts her again, from rear. One or both animal(s) utter(s) Squeaks as he mounts. Copulation. Female resists, but not violently. She just turns around to look at male. He dismounts, walks away. Female immediately assumes Arch Posture—and utters a series of Gulps! Then relaxes. Follows male around cage, 7:50. Then both animals retire to sleeping box . . .

7:56. Male is grooming female in box. This is accompanied by lots of sneezing by one or both animals . . .

8:02. Both animals come out of box. Sit side by side, facing in opposite directions. Female utters a few Squeaks. Then male begins to groom her. His movements are gentle. He devotes most of his attention to her lower back and rear. Female continues to utter Squeaks. Goes quite limp while male grooms. Possibly half asleep? Then she suddenly utters loud Squeaks, moves away from male. Goes into box. Male follows, continues Allogrooming in box . . .

8:17. Female apparently startled or annoyed by something. Bounces out of box, crouches in far corner of cage. Utters long series of Gulps. Male comes out of box, runs toward female, utters one Sneeze-grunt as he does so. Female runs back to box. Performs one burst of Rubbing movements in midst of run. Back into box. Male follows, resumes Allogrooming again . . .

The following extract illustrates the behavior of an inexperienced male.

January 28, 1962. O male and C female. This male has been hand reared, in partial isolation, ever since the age of approximately $1\frac{1}{2}$ months. Now full grown. Since being taken from his parents, he has had only brief contacts with other Night Monkeys. He is not familiar with C female.

7:00 p.m. Female let loose in male's cage. Male leaps away, freezes and crouches in far corner. Female explores cage, uttering Low Trills as she does so. Approaches male. The two animals sniff one another, nose to nose. Male utters Squeaks. Female moves away, resumes exploring with Low Trills. Approaches male again. He sniffs at her perineal region and utters more Squeaks. She moves away again. Explores with Low Trills. Approaches male again. He utters more Squeaks. She moves away again . . .

7:06. Female approaches male. He suddenly clasps her back, from the side, but does not mount. She breaks away and resumes exploring. Then approaches male again. A vicious fight breaks out. Male apparently the initiator, striking at the female with his hands. Lots of running, chasing, and striking during fight. Both animals quite silent throughout. Then they separate. Male retires to corner and assumes Arch Posture. Female walks around, not very rapidly, uttering many Gulps and a few Sneeze-grunts . . .

7:18. Male starts to approach female. She assumes an Arch Posture, starts to advance toward him. He retreats . . .

This sort of inconclusive behavior continues until 9:10, when I decide to stop observations. Then, happening to pass the cage at 9:50, I find the animals copulating! Resume observations.

Copulation apparently successful. Male dismounts. Then mounts again immediately. No preliminary display by either animal. Copulation again apparently successful. Pelvic thrusts at intervals of at least several seconds. Then male dismounts. No postcopulatory display. Male walks away a couple of feet.

Back to female almost immediately. Approaches her from side. Sniffs at her side and utters Squeaks. Climbs up onto her back, mounting from side. Once mounted, he seems to be trying to shift around into a copulatory position. Gets half way there, but female turns around to look at him, and he slides off. Then walks away again . . .

10:01. Male approaches female again. From side. Sniffs at her side and utters Squeaks. Half mounts, from the side. Then he begins to groom the female, while he remains sprawled sideways across her back. His grooming movements are extremely vigorous, even violent, and very awkward looking. Female just sits. Male eventually slides off. Remains sitting beside female, one hand resting on her back, and utters many Squeaks at irregular intervals. Female eventually walks away. Male follows . . .

10:10. Male grooms female steadily for several minutes. Reaching her from side. He repeatedly turns her half way over on her back, apparently trying to get at something under her arm on the far side. Both animals silent. Finally the female breaks away. Male follows her. Uttering Squeaks. Then mounts her from the rear. Tries to copulate. Copulation attempt probably unsuccessful. Only one or two pelvic thrusts. Both animals silent. Then male slips off . . .

10:19. Male approaches female again. Silently. Mounts her immediately, from rear. Copulation. Apparently successful. Long sustained, with many pelvic thrusts. Male finally dismounts. Sits beside female. She sniffs at his flank region. He immediately starts to groom her. Grooming lasts only a few seconds. Then male mounts again, from the rear. Copulation. Apparently successful. Many pelvic thrusts; the last one very long sustained and accompanied by quivering of the rear part of the body. Male slips off. Immediately starts to groom female again. This Allogrooming is much more prolonged and violent than the Allogrooming immediately before the last copulation.

10:22. Male stops Allogrooming momentarily. Then starts again. Grooming movements even more violent than before. Again and again he twists the female over on her back. No attempt to mount. Female silent; male utters occasional Squeaks. Then the male stops Allogrooming and walks away.

He goes back to the female almost immediately. Mounts her from the front, climbing over her head. Lies on her back, his head over her tail, his tail hanging in her face! He slips off after a few seconds, and the two animals separate . . .

This sort of behavior, including many copulation attempts (all apparently unsuccessful) and much violent Allogrooming by the male, continues spasmodically as long as I continue to watch the animals, until 11:00 p.m.

During this encounter, it was obvious that the male had a strong copulatory tendency, but he seemed to have difficulty in orientating

his copulatory movements, and he was certainly somewhat hostile to the female at first. (His awkwardness persisted for at least 5 nights. But shortly afterwards he was observed to perform sexual reactions quite smoothly.)

The last extract illustrates the behavior of pairs when the female is dominant over the male.

January 24, 1962. P female and Z male. These animals may have had some previous sexual experience; but they are not acquainted with one another. They have been kept isolated in separate cages for several days.

6:45 p.m. The male is let loose in the female's cage. The female rushes to him. They sniff one another, nose to nose. The female utters one Low Trill during sniffing. Then they separate. The male runs around the cage, possibly frightened. The female moves around more slowly. Neither animal is following the other. One or both always assume(s) an Arch Posture when they come close to one another.

6:50. The two animals settle down to a routine, which does not change very much for almost three hours.

The male retires to a corner of the cage, and sits quietly in a crouching freeze posture whenever he is left alone by the female. Sometimes his freeze includes a trace of a head-down component. After an hour or so, when the female starts to become less active (see below), he occasionally closes his eyes, briefly, while continuing to sit in the same posture most of the time.

The female approaches the male repeatedly. When she approaches him slowly, or at a normal running pace, she usually sniffs him. She usually begins by sniffing at his face, and then sniffs his side and/or his perineal region. When she sniffs at his side, she often appears to be trying to smell under his arm or in his armpit. Sometimes she seizes his hands, arms, or head, in order to pull him into the right position to facilitate sniffing the area she is interested in at the time. Sometimes she grooms the male immediately after sniffing. This occurs first during her third approach. It becomes increasingly frequent as the evening wears on.

Sometimes the male moves away after the female begins to sniff at him. Sometimes he just sits still. Most frequently, he sniffs in return. In most cases, he sniffs more briefly than she does. He often appears to be unwilling to sniff, but unable to resist the stimulus provided by the female. He usually sniffs her perineal region after sniffing her face (the animals are then nose to tail).

Most of this sniffing and Allogrooming is accompanied by Squeaks by the female. One or both animals also utter(s) a few Low Trills and many Moans. The Moans are uttered most frequently around 8:50-9:00 p.m., presumably when the animals are becoming accustomed to one another.

Sometimes the Allogrooming develops into a dispute. When the female grooms too energetically. The male strikes at her with his hands. Silently. When the male does this, the female always responds by "bombarding" him. She runs away from him, uttering many Gulps and a few Sneeze-grunts, turns, faces him, pauses a second, performs a few Rubbing movements, and then leaps at him. Usually she leaps just above him, landing on the side of the cage an inch or less above his head. Her tail usually slaps into his face as she lands. Occasionally she crashes into him full force with her whole body.

She usually performs several leaps one right after the other, before resuming slower approaches and Allogrooming . . .

The male does not respond to the female's leaps as strongly as might be expected. Usually he just sits quietly throughout. Occasionally (especially during the first hour) he assumes an extreme Arch Posture just as the female starts to leap. Once or twice he strikes at her, but he never chases her . . .

8:45. The male starts to relax a little. Occasionally starts to follow the female when she goes down to the floor of the cage to get food . . .

9:45. The two animals are sitting side by side. Then the female goes down to the floor, picks up a piece of fruit, climbs up to a branch, about three feet from the male, and starts to eat. The male walks toward her slowly. Sniffs at her perineal region. Then suddenly mounts her, from the rear. Slightly awkward. The female does not lift her tail, so the male has to shift his body in order to insert his penis from the side. Copulation. Apparently successful. Several pelvic thrusts at irregular intervals. The female leans downward and forward during the copulation, still clutching food in her hand. Then the male dismounts. Sits beside female, facing in the same direction. Then turns around, sniffs at her perineal region again, mounts her again, and copulates again. Again apparently successful. Then he dismounts and sits beside the female as before. She calmly finishes eating her food, turns around, and sniffs his perineal region. Then both animals sit quietly . . .

BEHAVIOR OF YOUNG ANIMALS

Three baby Night Monkeys were born, to different parents, in captivity on Barro Colorado Island. One of these was left with its parents, but died when approximately 2 months old. The second was taken from its parents at the age of $1\frac{1}{2}$ months, and raised by hand. The third was born only 9 weeks before this paper was written, and was left with its parents. Several other infants were bought in the Panama market, and hand raised successfully in captivity. Many of the other individuals kept in captivity on Barro Colorado Island were secured when they were still subadult. A few subadult individuals were observed in the wild on Barro Colorado.

The infants born in captivity on Barro Colorado Island were not watched very much while they remained with their parents, as it was feared that prolonged observation might disturb the parents unduly and cause them to abandon or neglect the young. It was only possible to note a few aspects of the parent-infant relationship.

For the first few days after birth, the infant is always carried by the mother, clinging to her breast or belly. Later it usually rides on the back of a parent.

Male Night Monkeys seem to play an important role in raising their offspring. Before they were 3 weeks old, two of the infants born in captivity on Barro Colorado Island were being carried by

their fathers most of the time when they were not actually being suckled by their mothers. The third infant was certainly carried by its father much of the time, but I could not determine exactly how much, simply because the father and mother were very difficult to tell apart (without catching them in the hand). This was the infant that was observed most frequently. It was first seen being carried by the father at the age of 9 days. This was also the first time that it was seen riding on the back of a parent. (It seems probable that these two developments were causally related. But carrying on the back is not a purely masculine pattern. The same infant sometimes rode on its mother's back before and/or after being suckled.) I was informed by a keeper at the National Zoological Park that a baby Night Monkey born to a captive pair there, and raised by its parents, also usually was carried by the father.

This parental behavior is interesting from a comparative point of view. Infants and young apparently are always carried by their mothers, as long as they are carried at all, in such genera of New World primates as *Alouatta* and *Ateles* (Carpenter, 1934 and 1935). The only other platyrrhines in which the father is known to carry the young regularly are the marmosets and tamarins (Sanderson, *op. cit.*, and Hill, 1957).

There is at least one published record of a male Titi Monkey, *Callicebus*, carrying young (L. E. Miller, quoted in Allen, 1916); but it is not known if the habit is regular in the species.

Hill's (1960) statement that Allen (in the same paper) cited evidence to show that male *Saimiri* frequently carry young is apparently erroneous.

The carrying of young by males may be primitive among Platyrrhine and/or an indication of close phylogenetic relationship between Night Monkeys and marmosets and tamarins. (Night Monkeys resemble marmosets and tamarins in a number of other characteristics.) In any case, such behavior must be adaptive. Its principal advantage may be the sharing of labor. When the male carries the young part of the time, neither parent will become as exhausted and "run-down" (and therefore susceptible to predators and disease) as the female would be likely to become if she did all the work herself. (Even if the male has the harder job because he carries the young most of the time, he can support the strain better than his mate simply because he does not have to produce milk. Males may get less tired also because they are usually, or perhaps always, slightly larger and more powerful than their mates.)

In all probability, the advantages of such behavior can be secured only when the sex ratio is effectively one to one and the pair-bonds between mates are close and long sustained. Species of *Alouatta* and *Ateles* probably cannot afford such behavior because they usually live in groups in which there are more females than males. There may occasionally be more infants than adult males in such groups. The looseness and brevity of pair-bonds among howlers must also tend to prevent the establishment of continuous bonds between males and infants. Infants must be fed by their mothers at more or less frequent intervals, and regular transfers from one parent to the other might be difficult to arrange when the parents do not stick together.

Thus, the type of parental behavior shown by Night Monkeys in captivity would seem to provide strong support for the hypothesis that males and females of this species usually form pair-bonds which are at least moderately long sustained under natural conditions (see page 12).

Like all baby monkeys, infant Night Monkeys have very strong clutching tendencies and try to keep in close physical contact with a parent at almost all times. The only exceptions occur when an infant moves from one parent to another before and after feeding (see next paragraph). When clutching a parent, an infant usually uses both hands and feet to hold on to the parent's fur, and may also keep its tail pressed against the parent's body. The infant born in captivity that was observed most frequently was very inactive, aside from feeding, during the first few days of its life. By the time it was 3 weeks old, however, it sometimes moved around most energetically on its parent's back.

My observations would suggest that an infant usually shifts from one parent to the other, at feeding time, under its own power. The parents do not lend a hand to lift or support the infant during the transfer unless it should start to fall.

The infants raised in captivity apart from their parents quickly learned to accept human beings as foster parents. They appeared to be almost perfectly satisfied to be carried by a human being, especially if they could ride on the head and clutch hair. Somewhat more slowly and reluctantly, they also learned to accept turkish towels as parent substitutes. An infant conditioned in this way usually spent all its time clutching its towel (unless it had to leave the towel to feed or drink).

Except when specifically stated otherwise, the behavior patterns of infants and juveniles described hereafter in this section were performed by young animals hand reared in captivity, after being sepa-

rated from their parents. All these individuals were at least $1\frac{1}{2}$ months old.

A perfectly content infant, with all its desires satisfied, is silent and motionless (and usually asleep). Sounds and movements are apparently always indications of dissatisfaction. When an infant is slightly dissatisfied, it may begin either movements or sounds first, or both together. (It is my impression that an infant is most likely to move without vocalizing when it "knows" in advance that it can remove its dissatisfaction by its own efforts.) The first movements may be nothing more than slight readjustments in the position of the limbs or other parts of the body. At higher intensities of dissatisfaction, the infant usually goes straight to whatever individual or object it expects will be able to satisfy its need (*e.g.*, a food dish when it is hungry) or, if this is not possible, makes vigorous searching movements.

The hand-reared infants apparently never moved about just for the sake of moving. They did not seem to have any trace of the independent locomotory tendency of adults. All their movements appeared to have an immediate "practical" end in view apart from the mere performance of the movements.

By far the most common vocal patterns of infant and young juvenile Night Monkeys are Squeaks and Squeaklike notes. A typical "pure" Squeak is brief, not very loud, and much higher in pitch than any of the Grunt Complex patterns. Sketches of sound spectrograms of pure Squeaks are shown in figures 15, 17, and 18. Each pattern of this type sounds like a single note to human ears. The sound spectrograms, however, indicate that at least many of the pure Squeaks are actually partly or wholly compound, composed of two or three sounds separated by *very* short intervals or two or three partly distinct "syllables." It will be convenient to refer to such patterns in terms similar to those applied to the equally compound Hoots described above. A pattern that sounded to me like a single note will be called "a Squeak" or "a note." The various sounds which spectrograms may show to be included in a single Squeak, in this sense, will be called "components of a Squeak."

All the accompanying sketches of vocal patterns by an immature individual are based upon recordings of a single male who was exactly 45 days old at the time of recording.

The pitch of a single Squeak seldom or never remains level throughout. In most cases, the pitch first rises and then falls. When a Squeak is composed of two more or less distinct components, the rise usually extends throughout the first component and the fall throughout

the second component. The rate of rise or fall may vary within the same component. When a Squeak is composed of three more or less distinct components, the first usually rises, the second usually rises or remains approximately level, and the third usually falls. More rarely, the pitch may rise or fall more or less steadily throughout a whole Squeak, or may first fall and then rise.

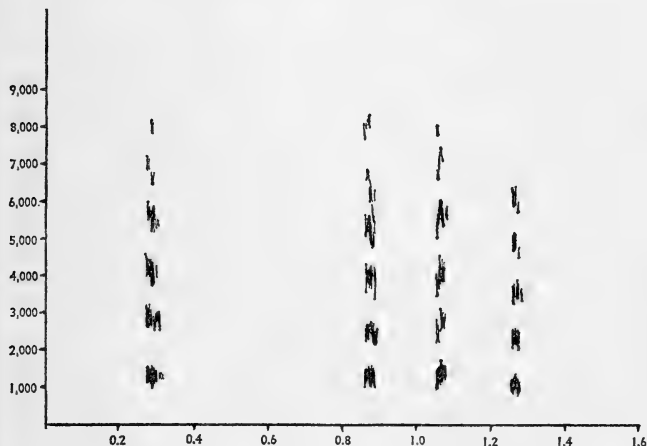


FIG. 15.—Four typical "pure" Squeaks, uttered by an immature.

Based upon a spectrogram by a "Sona-graph."

Some Squeaks are much louder than usual without being prolonged. Patterns of this type tend to extend over a particularly wide range of pitch (see figure 16).

In some Squeaks with both rising and falling pitch the rising part is loudest; in others the falling part is loudest.

The Squeaks of infants and young juveniles intergrade with both Screams and High Trills.

The "pure" Screams of infants and young juveniles sound similar to adult Screams, but are slightly softer and perhaps slightly plaintive in tone. The most extreme Screams of the young animals that I studied sounded as if they were approximately as long as the adult Screams shown in figure 5, and only slightly higher in pitch on the average. It is possible that infants and juveniles never utter Screams of as long duration as the adult patterns shown in figure 6; but I

never subjected any young individual to the stresses which would be expected to produce the highest intensity type of Screaming.

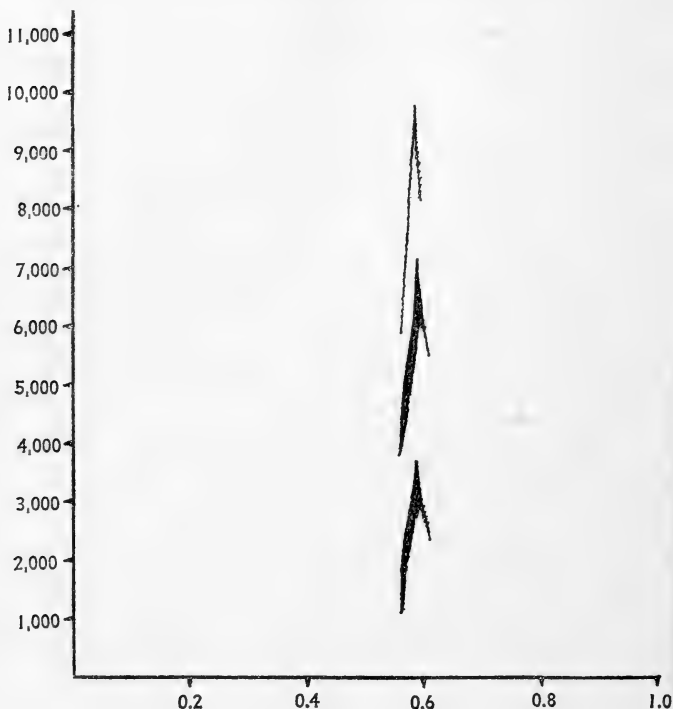


FIG. 16.—A single very loud Squeak, uttered by an immature.

Based upon a spectrogram by a "Sona-graph."

There were at least three more harmonics with this note that are not shown in the drawing.

Patterns intermediate between pure Squeaks and pure Screams are variable, but always more or less intermediate in length and sometimes slightly higher in pitch, on the average, than the lowest Squeaks. They also tend to fluctuate, rise and fall slightly in pitch, in much the same way as pure Screams, but the number of fluctuations is less than in the latter. Sometimes an intermediate pattern retains a trace

of the slight (inaudible to human ears) division into separate components which is characteristic of many Squeaks. Figure 17 includes a pattern of this type. The intergradation between pure Squeaks and pure Screams seems to be complete, insofar as infants and young juveniles utter every possible type of morphologically intermediate pattern.

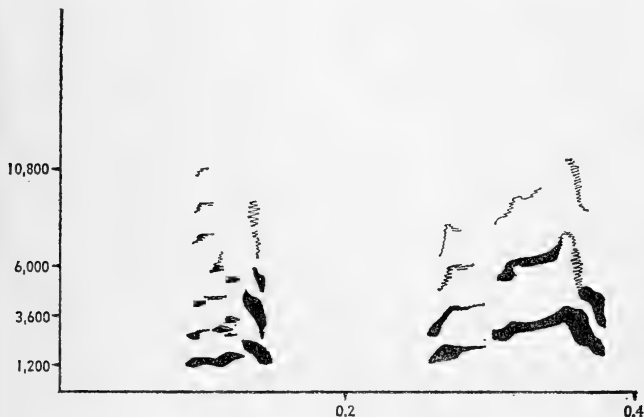


FIG. 17.—A "pure" Squeak, followed by a longer note more or less perfectly intermediate between a Squeak and a short Scream. Uttered by an immature.

Based upon a spectrogram by a "Vibralyzer."

Compare with the Scream shown in figure 5 and the Trills shown in figure 19.

"Pure" High Trills are conspicuously compound. To human ears, each High Trill sounds as if it were composed of three or four Squeaks uttered in rapid succession. Most sound spectrograms convey the same impression. A sketch of a more or less typical pure High Trill is shown in figure 18. The successive notes in a single High Trill are seldom exactly the same pitch. In most cases, the first one or two notes are largely or completely rising and the last one or two notes are largely or completely falling.

A remarkable feature of the vocal repertoire of young Night Monkeys is that the arrangement of components within a single Squeak, *i.e.*, the sequence of changes in pitch and the relative distance between high points and low points is sometimes similar to the arrangement of successive Squeaks within a single High Trill. Thus, the

form of a pure High Trill may be essentially similar to that of a pure Squeak, only on a much longer time scale. The sequence of rises and falls in pitch within a single short Scream may be equally similar to the arrangement of the corresponding features within both a single Squeak and a single High Trill.

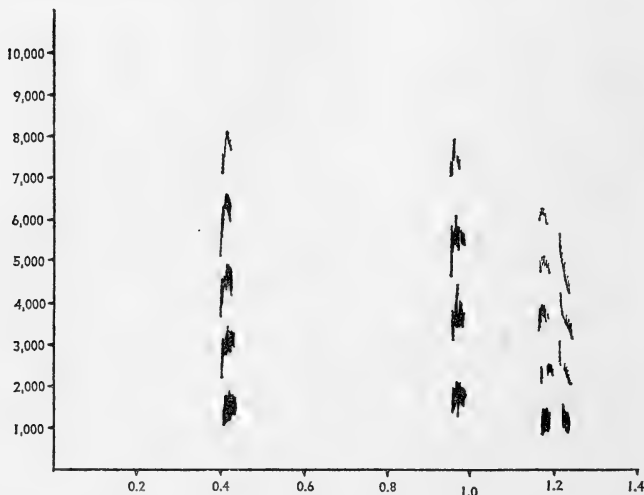


FIG. 18.—A series of four notes uttered by an immature.

Based upon a spectrogram by a "Sona-graph."

This series sounded, to me, like one "pure" Squeak followed immediately by a short High Trill. As a whole, it is comparable to the series shown in figure 15, which sounded as if it were composed of four separate Squeaks.

Therefore, although most High Trills appear to be, or sound as if they were, accelerated series of several Squeaks, the same morphological effect might be produced by slowing down a single Squeak in such a way that the individual components within it become more distinct and widely separated from one another. Similarly, the effect of a short Scream could be produced either by slowing down and lengthening a single Squeak, while maintaining or strengthening the connections between its components, or by letting a series of several Squeaks "run together." In other words, many or most High Trills could be interpreted as discontinuous series of either Squeaks or components of Squeaks, while many or most short Screams could be

interpreted as continuous series of either Squeaks or components of Squeaks. (These relationships are difficult to describe or explain verbally, but I think that they will become clear if the accompanying drawings of sound spectrograms are studied in detail.)

In view of these facts, it is not surprising that the patterns intermediate between pure Squeaks and pure High Trills appear to be somewhat heterogeneous. Some intermediates are moderately rapid series of a few obviously distinct notes, apparently series of Squeaks which are not accelerated as much as the components of pure High Trills. Others are brief patterns which sound rather like single Squeaks with faint "rattling undertones." These may be Squeaks in which the internal components have become more distinct from one another than in typical pure Squeaks. The two intermediate types intergrade with one another. It is my impression, in fact, that the intergradation between pure Squeaks and pure High Trills is as complete as the intergradation between Squeaks and Screams.

Infant and juvenile Night Monkeys also utter many patterns that seem to be intermediate between Screams and High Trills. These are all more or less prolonged, discontinuous, and wavering. Figure 19 is a sketch of two patterns of this type (somewhat nearer to pure High Trills than to pure Screams). At least equally common are patterns that appear to be intermediate between High Trills, Screams, and Squeaks. These are similar to the intermediates between High Trills and Screams but shorter.

It is evident, therefore, that the patterns which have been called pure Squeaks, pure Screams, and pure High Trills in the preceding discussion are merely the extreme points of a continuum. This whole group of patterns may be called the "Squeak Complex."

It seems probable that all the vocal patterns of both adult and young Night Monkeys can be included in either this complex or the Grunt Complex.

The mouth is opened to a moderate extent during all or most notes of the Squeak Complex (see figure 22).

Infants raised apart from their natural parents utter Squeaks and intermediate notes closely similar to pure Squeaks very frequently whenever they are not clutching a foster parent or parent substitute (if they are not "distracted" by food or drink). A tame infant which has been silent while being carried by a human being will always begin to utter Squeaks (with or without other notes—see below) as soon as it is lifted away. It may also start to move in an obvious attempt to follow and rejoin the human being. Its Squeaks may become louder and more rapid if the human being then disappears from sight.

These facts would suggest that many or most of the Squeaks uttered by infants are produced when their tendency to keep in physical contact with a parent is thwarted.

This may not, however, be true of all their Squeaks. Infants clutching a foster parent or parent substitute may also utter Squeaks just before shifting the position of their limbs of their own accord, *i.e.*, before they can have lost contact. Once, an infant which had

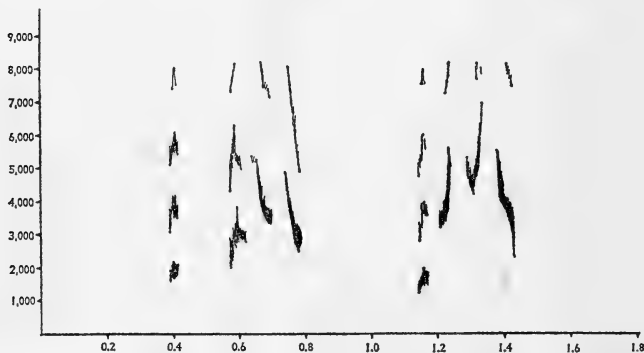


FIG. 19.—Two loud trilling patterns, intermediate between “pure” High Trills and Screams, but most similar to the former. Uttered by an immature.

Based upon a spectrogram by a “Sona-graph.”

Each trilling pattern is a series of four notes or groups of components. Each of these series seems to be similar to the series shown in figures 15 and 18, and to the components of the single Squeak and the intermediate between a Squeak and a Scream shown in figure 17.

Additional harmonics, up to at least 18,000 c.p.s., accompanied these trilling patterns, but are not shown in the drawing.

been quite silent while riding on my head suddenly began to utter Squeaks when rain began to fall, in spite of the fact that it continued to clutch me tightly.

Such incidents would suggest that infants may utter Squeaks whenever they become “uncomfortable” or feel “frustrated” in any one of several different ways. If so, their Squeaks can be considered a generalized distress reaction, strictly comparable to the “distress calls” of many young birds.

Of all the other platyrrhines I know, only infant tamarins of the genus *Saguinus* utter distress notes as frequently as infant Night Monkeys in similar circumstances.

Under natural conditions, it seems likely that the parents of an

infant Night Monkey would respond to its Squeaks by trying to make it more comfortable, *e.g.*, by helping it to readjust its position or by feeding it.

Unfortunately, this could not be checked by observation of the infants raised by their own parents in captivity. The parents of both infants seemed to be attentive and conscientious, and the infants were silent most of the time, presumably because they were seldom sufficiently uncomfortable or thwarted in the right way to induce vocalizations. I did hear them utter a few Squeaks, quite like those of the hand-reared infants. They uttered these notes in a variety of circumstances, *e.g.*, while moving around on a parent's back, while trying to suckle, and (once) after falling off a parent's back. In most cases, the infants stopped vocalizing almost immediately, before the parents reacted. They apparently managed to achieve satisfaction by their own efforts. The infant that fell was retrieved by a parent, but I could not determine if this parental act was a response to the infant's Squeaks and/or to the scrambling movements that it made at the same time.

The fact that high-pitched notes will not carry as far as low-pitched notes has already been mentioned. It seems highly probable that the Squeaks of infants, like those of adults, are primarily short-range signals. Under natural conditions, they are probably almost always uttered by infants at least fairly close to their parents.

It is my impression that the Squeaks of both adults and young are slightly "ventriloquial." In the dark, I found it difficult to tell exactly where Squeaks were coming from. Their source was more difficult to locate than that of any other vocal pattern of the species (with the possible exception of some High Trills).

These features may be particularly advantageous because individuals uttering Squeaks may be so intent upon the activity in which they are engaged, or so distressed, that they may become less alert than usual to outside stimuli and fail to note the approach of a possible predator.

Infants may utter Squeaks (and/or closely related short intermediate notes) singly or in unaccelerated series (*i.e.*, series that are not at all Trill-like) of up to seven or eight notes. Longer series presumably are produced by greater distress than shorter series. Series are frequently repeated with only brief intervening pauses.

Infants also utter many series of notes which include both brief Squeaks or Squeaklike notes and longer Screams or Screamlke notes. The arrangement of notes in such series is quite variable. One common arrangement is three or four long notes followed immediately

by two or (less frequently) three short notes. Another common arrangement is four or five short notes followed immediately by a single long note. Other and more or less intermediate arrangements also occur, but seem to be somewhat less common.

Infants may "settle" on one particular type of mixed series, and repeat it without variation in form for appreciable periods of time, even when there is reason to believe that the strength of their motivation should be changing slightly. They sometimes seem to become "stuck in the same groove." This would suggest that the utterance of one type of series may facilitate repeat performances of the same series, but does not facilitate, and may even discourage, subsequent performances of different types of mixed series composed of the same notes in different sequence.

Some of the Screams and intermediates between Screams and Squeaks uttered by infants may contain a hostile component like the Screams of adults. The infant born and hand raised in captivity on Barro Colorado Island uttered many Screams and related intermediate notes during the first few days after being taken from its parents, a period during which it also performed an appreciable number of overtly and unmistakably hostile reactions. Infants also tend to utter Screams when handled somewhat roughly. But other Screams and intermediate notes are almost certainly not hostile. It was very common, for instance, to hear a captive infant which had accepted human beings as foster parents utter many notes of this type in immediate association with both Squeaks and Hoots (see page 75) when left alone. These notes were not accompanied by any trace of overtly hostile movements or Gruff Grunts, and both the Squeaks and the Hoots were certainly provoked by the thwarting of the infant's desire to be with its foster parents. It seems likely, therefore, that at least many of the patterns intermediate between Squeaks and Screams are similar to the former in being generalized distress reactions. This, and the complete intergradation between the two extreme types of patterns, would suggest that the Screams of infants are little or nothing more than the highest intensity form of their Squeaks. (It would not, in fact, be necessary to give the patterns different names if they were not so distinct, in both form and causation, when uttered by adults).

The captive infants uttered High Trills when approaching their food dishes and feeding, and also when I lifted them up and brought their faces close to mine. This would suggest that their High Trills were produced by the same motivation as some or all of the Trills of

adults and/or by the same factors as their own Squeaks plus an added component of alarm or escape.

Some of the brief Squeaks or Squeaklike patterns of infants have a slight "gulping" quality. They may be the source from which the Gulps of adults are derived in the course of ontogeny; but they certainly are not distinctive or well segregated when uttered by infants.

Infants utter Hoots occasionally. To human ears, these sound very much like slightly softer versions of the usual Hoots of adults; but sound spectrograms indicate that they are sometimes (at least) also higher pitched and more broken up (see figure 20). They are usually

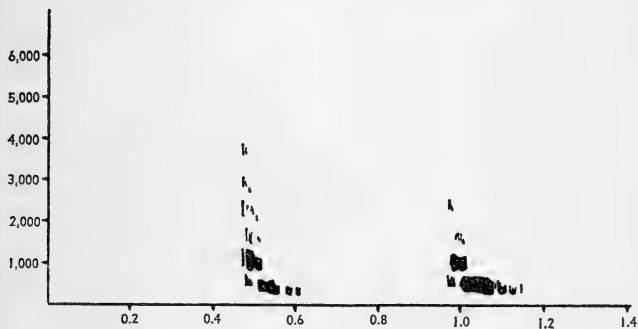


FIG. 20.—Two Hoots, uttered by an immature male.

Based upon a spectrogram by a "Sona-graph."

uttered in series of two or three notes, apparently always when an infant has become separated from its parents or parent substitute. Like adults, infants usually or always sit still while uttering Hoots. Their Hoots seem to be high-intensity patterns, produced when their desire to be with a parent is stronger, or more strongly thwarted, than when Squeaks or related intermediate notes are uttered. Thus, for instance, an infant suddenly separated from its foster parent or parent substitute may utter Hoots, intermediates between Squeaks and Screams, and more or less pure Squeaks at first, then stop uttering Hoots but continue the other notes, then stop the Screamlke notes but continue Squeaks, and finally fall silent, as it gradually becomes accustomed to being alone. Similarly, an infant accustomed to being carried almost steadily by a foster parent is apt to utter relatively more Hoots and fewer Squeaks than an infant used to being carried only occa-

sionally, when both are separated from their foster parents in similar circumstances and with the same degree of abruptness.

(It is interesting that the vocal patterns uttered by infants who want to attract or join their parents are similar to those of adults who want to attract or copulate with their mates. This might suggest that the sexual tendencies of adults develop from the infantile tendency to keep in contact with parents.)

The lowest intensity Hoots of infants (uttered toward the end of a period during which Hoots have become progressively less frequent)

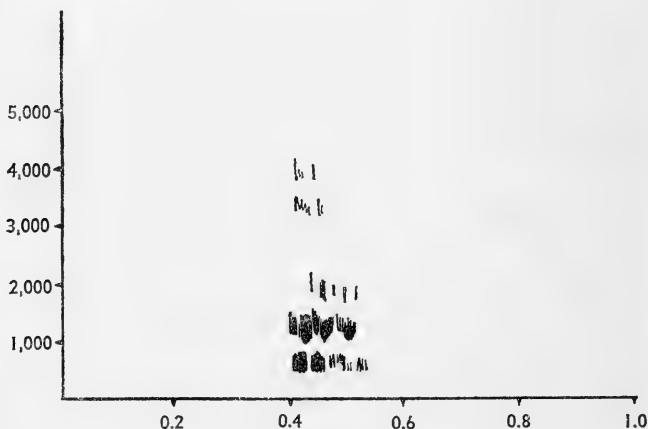


FIG. 21.—A single "Brrrrp" sound, uttered by an immature.

Based upon a spectrogram by a "Sona-graph."

This drawing does not show all the harmonics present.

are relatively very soft and somewhat reminiscent, to human ears, of the Moans of adults. The two types of patterns may be related ontogenetically.

The infant whose calls were recorded was heard to utter a few, rather low-pitched, rattling sounds (see figure 21). These sounds were relatively very rare, and were not heard to be uttered by other individuals. It seems probable that they were more or less "abnormal" variants of some more common pattern. They sounded, to me, as if they could be intermediate between High Trills and Gruff Grunts; but spectrograms suggest that they were related to Hoots. They may

have been incompletely formed Hoots, uttered without proper adjustment of the vocal apparatus.

That this sort of variation is possible is indicated by the behavior of howler monkeys. Male howlers usually utter lengthy roars at dawn.



FIG. 22.—An infant uttering Squeaks.

This shows the characteristic shape of the mouth when opened most widely during vocalizations of the Squeak Complex.

When fully developed, each roar sounds absolutely continuous. But males of the species on Barro Colorado (*Alouatta palliata*) seem to take considerable time to "warm up," and their first attempts to roar are apt to come out as wooden-sounding rattles (these may be the sounds that Altmann, *op. cit.*, describes as "pops").

Infants utter Gruff Grunts which sound quite like the corresponding notes of adults and occur in similar hostile circumstances. They

also try to bite when handled, and perform other overt unritualized attack and escape patterns like those of adults as soon as they have developed adequate coordination of the limbs.

Changes in behavior between the infantile stage and maturity were not studied in detail, as it was not considered advisable to do much experimental work with the young animals being raised in captivity. (In any case, there are indications that at least some patterns develop at different rates in captivity and in the wild—see above.) Intermittent observations of the captive animals did, however, reveal the following.

The young animals gradually lost their desire to be carried by a parent. This process seemed to be completed by the time that they were approximately half grown (at the age of 6 or 7 months). By the time that they were a year old, they usually objected violently to being touched by the human beings whom they had regarded as parents earlier.

It was my impression that all or most of the signal patterns of young animals were essentially the same as those of adults by the time that they were half grown, with the exception of the strictly sexual patterns and the Squeaks. The young animals continued to direct many Squeaks toward human beings with whom they were familiar until they were approximately 1 to 1½ years old. All or most of the later Squeaks seemed to be essentially friendly "greeting" patterns. Many of them were closely associated with social sniffing.

The obviously subadult individuals observed in the forest on Barro Colorado Island also tended to utter more Squeaks than adults.

Two immature Night Monkeys at Iquitos performed a variety of signal patterns in addition to the Hoots already mentioned. They were observed to perform Swaying and to utter typical Gruff Grunts and Screams like those of adults on Barro Colorado Island. They also uttered many Squeaks like those of young animals of similar age (or stage of development) on Barro Colorado.

PREVIOUS DESCRIPTIONS OF NIGHT MONKEY BEHAVIOR PATTERNS

A number of signal patterns of Night Monkeys have been described, more or less briefly, in previous publications. Some of these descriptions have been cited above. It may be useful, however, to mention some others, try to identify and classify the described patterns according to the terminology used in this paper, and discuss some apparent discrepancies and problems.

Hill (1960) summarizes several accounts by earlier observers and quotes some of their transcriptions of vocal patterns. The notes variously transcribed as "oo-oo-oo," "bu-bu-bu," and "boom" may be the same as the notes I have called Hoots. The notes transcribed as "chip-chip-chip," "chuip-chuip," and "kweep-kweep" presumably are Squeaks. The notes transcribed as "urr-urr" may be Gruff Grunts.

Sanderson (*op. cit.*) says that a Night Monkey that he kept in captivity uttered "grrrrrrmph" notes as a sign of contentment or pleasure. His transcription would suggest that the notes were Grunts; but, if so, his interpretation of their significance is almost certainly wrong. He may have been misled by the fact that captive Night Monkeys sometimes utter many Gruff Grunts without extreme or immediately recognizable attack and escape movements, *after* they have learned that such movements do not produce the desired results, *i.e.*, after they have learned that they cannot get out of their cages or force their captors to retreat permanently.

Sanderson mentions a variety of other sounds, all or most of which are unidentifiable. He also says that no two individual Night Monkeys have the same repertory of sounds. This is not only extremely improbable *per se*, but is not borne out by my own observations. All Panamanian Night Monkeys probably utter almost exactly the same types of sounds, although there may be slight differences (in pitch, length, or loudness) between the equivalent sounds of different individuals, and different individuals may utter the same sounds in slightly different situations, presumably because they have had different histories. (All the more or less distinctive notes and calls which were heard uttered by only one individual were extremely rare; and it seems likely that further observations would have shown that they are also present in the repertories of other individuals.)

The most extensive published descriptions of Night Monkey calls are by Andrew (*op. cit.*). His account is based upon observations of two individuals in the laboratory. Unfortunately, he does not say where his animals came from or describe the conditions in which they were kept. As a result, it is difficult to interpret some of his findings.

All or most of the patterns that he calls "twitters" would seem to be varieties of what I have called Squeaks. So, in all probability, are the notes that he calls "guinea-pig squeaks." (It may be worth mentioning that none of the Squeaks or Squeaklike notes of the individuals kept on Barro Colorado appeared to have "traces of clicks" like those which Andrew describes as being superimposed upon twitters.) The patterns which Andrew calls "trills" may be "High Trills" according

to the terminology used here. (His account would suggest that the individuals that he studied were either young or adults which had retained juvenile characteristics.) The patterns which he calls "waver-ing squeaks," "sharp calls," and "booms" are not precisely identifiable, although the latter two (at least) would appear to belong to the Grunt Complex.

One further comment may be added. There may be some geo-graphic variation in the form of some vocal patterns of Night Mon-keys; but it seems unlikely that the differences between the patterns of different populations or subspecies are as great as might be inferred from some of the published accounts.

SUMMARY

This is the first in a series of papers on the social signals and some other behavior patterns of New World primates.

Night Monkeys are moderately small. Under natural conditions, they are purely arboreal and nocturnal. In Panama, at least, they are not very gregarious. They are seldom found in groups larger than a single family of two adults and one young, and even mated individuals may stray some distance apart from one another.

The hostile behavior of adult Night Monkeys includes unritualized attack and escape movements and a variety of ritualized displays. A few of these displays are special postures and movements, *i.e.*, visual signals, but the great majority are notes and calls, *i.e.*, auditory signals. The sexual behavior of adults includes olfactory and tactile signals in addition to unritualized patterns and a few auditory signals.

Some of the most distinctive features of this display behavior seem to be direct or indirect consequences of, or adaptations to, nocturnality.

Adult Night Monkeys have fewer visual displays than any other platyrrhines whose behavior has been studied. The few that they do have are relatively crude, produced by simple movements of the whole head and/or body. Some of their visual displays are less exaggerated in form than the homologous patterns of related species. They do not have any facial expressions, or erectile tufts or ruffs of hair around the face which could be used in signaling. It seems likely that they have lost, or failed to develop, an extensive and complex system of visual signals simply because they frequently cannot see one another clearly in the forest at night.

As partial compensation, they utter "contact notes" more frequently than other platyrrhines. These may help to maintain social cohesion between the adult members of a family group in the dark.

The whole vocal repertory of adult Night Monkeys is composed of discrete units, nine or ten distinctly different types of notes and calls. These patterns do not intergrade with one another to any appreciable extent. Intermediates between different types of notes and calls are comparatively (if not always actually) rare. Complex messages are given in the form of series of different notes or calls, each one of which contains part of the message, not in the form of a single intermediate or ambivalent note or call containing the whole message in itself. This type of vocal repertory is quite different from that of any other monkey whose behavior has been described. It is also quite different from the repertory of infant and young juvenile Night Monkeys. It may be an adaptation to ensure that vocal messages cannot be misinterpreted, even when they are not accompanied by any relevant nonvocal information. In many circumstances, adult Night Monkeys must have to react to, and rely upon, vocalizations alone.

There may be a general rule, among all monkeys, that species or classes of individuals that are largely dependent upon auditory signals for the regulation of their social behavior tend to have discrete, sharply delimited vocal patterns, while species or classes of individuals that are less dependent upon auditory signals tend to have intergrading vocal patterns.

Most vocal patterns of adult Night Monkeys are very low pitched. They are lower on the average than those of any related species of similar size. As low-pitched sounds should carry farther than high-pitched sounds, this may be another adaptation to ensure that vocal messages are as clear as possible. The only high-pitched vocal patterns of adult Night Monkeys are short-range signals.

Some peculiar negative features of the behavior of adult Night Monkeys may be correlated with their slight degree of gregariousness. Unlike adults of many related species, they seldom perform "Allogrooming" (the grooming of one individual by another) except in copulatory situations, or perform redirection attacks upon other individuals of their own species. They also seem to lack vocal patterns whose primary or only function is to warn other individuals of possible danger in the environment.

Other distinctive features of the species include: Care of the young by the male (this may be possible only because the sex ratio is one to one and pair-bonds are close and long sustained); comparatively frequent use of the hands during fighting (possibly because the canine teeth are small); the apparent absence of any tendency to

jump up and down and break off branches in rage (this may be correlated with the small size of the species); and the apparent absence of "displacement" scratching or grooming.

Most of the vocal patterns of infants are high pitched and completely intergrading. Infants may be able to afford such behavior because they are always in close contact with their parents. The effects of their vocalizations may be supplemented and reinforced by tactile and visual stimuli.

Some of the display patterns of Night Monkeys are particularly reminiscent of howler monkeys (*Alouatta*), titi monkeys (*Callicebus*), and/or tamarins (*Saguinus*).

ACKNOWLEDGMENTS

I am greatly indebted to many people for assistance in studying the vocal patterns. In particular, Dr. W. John Smith helped with the recordings, made the spectrograms on the "Sonagraph," and contributed many useful suggestions and criticisms. D. K. North and Miss J. Arnold provided technical assistance. The other spectrograms were made by Martin S. Brewer; I must thank Mrs. Helen Hayes for helping to arrange this. Dr. Brian Patterson and Dr. A. S. House gave helpful advice and explained some puzzling features of the spectrograms. Dr. J. D. Pye very kindly provided assistance and equipment in an effort to detect ultrasonic notes or calls.

I am also grateful to Dr. Theodore H. Reed and J. Lear Grimmer for facilitating work in the National Zoological Park, to Charles Hawkshead for permitting me to observe his animals in Iquitos, to Richard W. Thorington, Jr., for useful information on the skin glands of Night Monkeys, and to Dr. John H. Kaufmann and David Fairchild, 2d, for assistance in the field and in the laboratory on Barro Colorado Island.

BIBLIOGRAPHY

ALLEN, J. A.

1916. Mammals collected on the Roosevelt Brazilian Expedition, with field notes by Leo E. Miller. Bull. Amer. Mus. Nat. Hist., vol. 35, pp. 559-610.

ALTMANN, STUART A.

1959. Field observations on a howling monkey society. Journ. Mamm., vol. 40, pp. 317-330.

ANDREW, R. J.

1963. The origin and evolution of the calls and facial expressions of the primates. *Behaviour*, vol. 20, pp. 1-109.

BASTOCK, M.; MORRIS, D.; AND MOYNIHAN, M.

1953. Some comments on conflict and thwarting in animals. *Behaviour*, vol. 6, pp. 66-84.

BENNETT, C. F., JR.

1963. A phyto-physiognomic reconnaissance of Barro Colorado Island, Canal Zone. *Smithsonian Misc. Coll.*, vol. 145, No. 7.

BIEGERT, JOSEPH.

1961. Volarhaut der Hände und Füße. In "Primatologia," ed. H. Hofer, A. H. Schultz, and D. Starck, II/1:3. Basel.

CABRERA, ANGEL.

1957. Catalogo de los mamíferos de America del Sur. *Rev. Mus. Arg. Cie. Nat. "Bernardino Rivadavia,"* vol. 4, No. 1, pp. 1-307.

CABRERA, ANGEL, AND YEPES, JOSÉ.

1940. *Historia natural Ediar; mamíferos sud-americanos*. Buenos Aires.

CARPENTER, C. R.

1934. A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comp. Psych. Monogr.*, vol. 10, No. 2, pp. 1-168.
1935. Behavior of red spider monkeys in Panama. *Journ. Mamm.*, vol. 16, pp. 171-180.

COLLIAS, NICHOLAS, AND SOUTHWICK, CHARLES.

1952. A field study of population density and social organization in howling monkeys. *Proc. Amer. Phil. Soc.*, vol. 96, pp. 143-156.

CULLEN, J. M.

1963. Allo-, auto- and hetero-preening. *Ibis*, vol. 105, No. 1, p. 121.

ENDERS, R. K.

1935. Mammalian life histories from Barro Colorado Island, Panama. *Bull. Mus. Comp. Zool.*, vol. 78, pp. 385-502.

HANSON, GLORIA, AND MONTAGNA, WILLIAM.

1962. The skin of primates. The skin of the owl monkey (*Aotus trivirgatus*). *Amer. Journ. Phys. Anthropol.*, vol. 20, No. 4, pp. 421-429.

HERSHKOVITZ, PHILIP.

1949. Mammals of northern Colombia. Preliminary report No. 4: monkeys (Primates), with taxonomic revisions of some forms. *Proc. U.S. Nat. Mus.*, vol. 98, pp. 323-427.
1958. A geographic classification of neotropical mammals. *Fieldiana: zoology*, vol. 36, No. 6, pp. 581-620.

HILL, W. C. OSMAN.

1956. Behaviour and adaptations of the primates. *Proc. Roy. Soc. Edinburgh*, vol. 66B, pp. 94-110.
1957. Primates. III. Pithecoidea, Platyrrhini. Edinburgh.
1960. Primates. IV. Cebidae, Part A. Edinburgh.

HILL, W. C. OSMAN; APPELYARD, H. M.; AND AUBER, L.

1959. The specialized area of skin glands in *Aotes* Humboldt (Simiæ Platyrrhini). *Trans. Roy. Soc. Edinburgh*, vol. 63, part 3, pp. 535-551.

HINDE, R. A., AND ROWELL, T. E.

1962. Communication by postures and facial expressions in the rhesus monkey (*Macaca mulatta*). Proc. Zool. Soc. London, vol. 138, pp. 1-21.

LORENZ, KONRAD.

1952. King Solomon's ring; new light on animal ways. New York.

MARLER, P.

1956. Behaviour of the chaffinch. Behaviour, Supplement 5, pp. 1-184.

MOYNIHAN, M.

1955. Types of hostile display. Auk, vol. 72, No. 3, pp. 247-259.

- 1962a. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Coll., vol. 143, No. 7, pp. 1-140.

- 1962b. Hostile and sexual behavior patterns of South American and Pacific Laridae. Behaviour, Supplement 8, pp. 1-365.

- 1963a. Display patterns of tropical American "nine-primaried" songbirds. III. The green-backed sparrow. Auk, vol. 80, No. 2, pp. 116-144.

- 1963b. Inter-specific relations between some Andean birds. Ibis, vol. 105, No. 3, pp. 327-339.

NOLTE, ANGELA.

1958. Beobachtungen über das Instinktverhalten von Kapuzineraffen (*Cebus apella* L.) in der Gefangenschaft. Behaviour, vol. 12, pp. 183-207.

PLOOG, D. W., AND MACLEAN, P. D.

1963. Display of penile erection in squirrel monkey (*Saimiri sciureus*). Animal Behaviour, vol. 11, No. 1, pp. 32-39.

ROHEN, JOHANNES W.

1962. Sehorgan. In "Primatologia," ed. H. Hofer, A. H. Schultz, and D. Starck, II/1:6. Basel.

ROWELL, T. E.

1962. Agonistic noises of the rhesus monkey (*Macaca mulatta*). Symp. Zool. Soc. London, No. 8, pp. 91-96.

ROWELL, T. E., AND HINDE, R. A.

1962. Vocal communication by the rhesus monkey (*Macaca mulatta*). Proc. Zool. Soc. London, vol. 138, pp. 279-294.

SANDERSON, IVAN TERENCE.

1957. The monkey kingdom; an introduction to the primates. New York.

SCOTT, JOHN PAUL.

1958. Animal behavior. Chicago.

SIMPSON, GEORGE GAYLORD.

1961. Principles of animal taxonomy. New York.

ULLRICH, WOLFGANG.

1961. Zur Biologie und Soziologie der Colobusaffen (*Colobus guereza caudatus* Thomas 1885). Zool. Garten, vol. 25, pp. 305-368.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NUMBER 6

A REVISION OF THE AMERICAN VULTURES OF THE GENUS CATHARTES

By
ALEXANDER WETMORE
Research Associate, Smithsonian Institution



(PUBLICATION 4539)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
AUGUST 14, 1964

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NUMBER 6

A REVISION OF THE AMERICAN VULTURES OF THE GENUS CATHARTES

By
ALEXANDER WETMORE
Research Associate, Smithsonian Institution



(PUBLICATION 4539)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
AUGUST 14, 1964

PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

A REVISION OF THE AMERICAN VULTURES OF THE GENUS CATHARTES

By ALEXANDER WETMORE

Research Associate, Smithsonian Institution

Turkey vultures, found widely throughout the Americas, though easily recognized in life or when freshly killed, pose many difficulties in identification when preserved as museum specimens. The color differences of the bare head and upper neck that separate the species, and in the case of the red-headed group some of the subspecies, change soon after death to a dull hue discouragingly similar in all. My personal interest in these birds began in 1920 when I first encountered the yellow-headed vulture in life in the Chaco of Argentina and Paraguay, and in the report on that expedition I ventured to publish a synopsis that covered what I had been able to learn of the genus as a whole (Wetmore, 1926, pp. 86-91). The subject has remained one of intriguing interest, in large part because of its difficulties, and I have continued to examine birds of the genus whenever possible. A preliminary account of the yellow-headed group has been covered in another study (Wetmore, 1950, pp. 415-417). The account that follows is based on data from several hundred museum skins, in addition to many observations on living individuals that I have seen and have collected during my expeditions in tropical regions.

In these studies I have been indebted to many individuals, among whom I should mention especially Mr. J. D. Macdonald and other authorities of the British Museum (Natural History) for privileges in connection with their collections, in particular the material that had been studied by Harry Kirke Swann. Dr. G. Rokitsky of the Naturhistorisches Museum in Vienna made arrangements that, in his absence, allowed me to examine the series of yellow-headed vultures in that institution. The collections in the American Museum of Natural History and the Chicago Natural History Museum have been of repeated assistance. I have to thank especially Dr. George H. Lowery, Jr., for the loan of specimens that included two of the new form described in this paper. Dr. Emerson Kemsies, in charge of

the bird collections in the Museum of the University of Cincinnati, very kindly made special arrangements that allowed study of the large series of vultures in the Herbert Brandt collection under his charge. Curators of other collections have aided in allowing examination and, when necessary, in the loan of skins for comparison with the series in Washington.

The account that follows is a summary of the characters and distribution of the species of the genus, with their geographic races.

CATHARTES AURA (Linnaeus): Turkey Vulture

Bare head and neck in adult birds in life red, in one race lined narrowly across the back of the cranium with yellowish or greenish white; skin of the side and front of the neck near its base smooth, without caruncles; upper hindneck in adult bare.

Found in the Americas from the northern temperate area of North America through the tropics to the temperate regions of the far south where these birds range to Patagonia, Tierra del Fuego, and the Falkland Islands.

CATHARTES AURA SEPTENTRIONALIS Wied

Cathartes septentrionalis Wied, Reise Nord-Amer., vol. 1, 1839, p. 162. (Fox River, near New Harmony, Indiana.)

Cathartes aura carolinensis "Townsend" Friedmann, U.S.Nat.Mus. Bull. 50, pt. 9, Sept. 29, 1950, p. 44. (Nomen nudum; lapsus calami for *Cathartes aura septentrionalis* as listed by C. W. Townsend, Mem. Nuttall Orn. Club, no. 5, Aug. 1920, p. 97.)

Characters.—Borders of lesser wing coverts paler than in other races, averaging wider, and therefore more prominent; distal secondaries with paler brown borders and tips; size large, wing 509-545 mm.

Measurements.—Males (43 specimens), wing 509-545 (526), tail 250-288 (267), culmen from cere 22.7-26.8 (24.6, average of 40), tarsus 61.7-73.0 (66.0) mm.

Females (35 specimens), wing 518-552 (535), tail 255-292 (275), culmen from cere 23.7-27.2 (25.3, average of 29), tarsus 61.7-73.0 (66.0) mm.

Range.—Breeds in eastern North America from eastern Minnesota (Itasca County, rarely), central Wisconsin (Oconto County, one record), south-central Michigan, southern Ontario, central New York, southwestern Massachusetts, and Connecticut, south through eastern Iowa, Missouri, and Arkansas to Louisiana, the Gulf coast, and southern Florida: Intergrades with *C. a. meridionalis* in Minnesota, Kansas, Oklahoma, and eastern Texas.

Winters from the Ohio Valley, central Maryland (rarely in the intervening mountains), and New Jersey south to southern Texas (Rio Grande City), the shores of the Gulf of Mexico east to southern Florida, and the southeastern Atlantic coast.

Recorded casually in southern Arizona (Pima County), Quebec, New Brunswick, Nova Scotia, Labrador, Newfoundland, eastern Massachusetts, Vermont, New Hampshire, and Maine: Accidental in Bermuda (one record, December 1853).

Remarks.—The paler appearance of the wing coverts, due to the broad, light brownish-gray edgings of the individual feathers, separates this form from the western race *meridionalis*, in which many individuals are of equal size. Measurements of *septentrionalis* from birds taken during the breeding season indicate a cline from the smallest in Florida to the largest in the northern area of the range. The smaller individuals in the resident group in southern Florida are within the upper limits of the size range of *Cathartes aura aura*, but all that I have seen have the paler margins of the wing coverts of *septentrionalis*. The large northern individuals move in winter throughout the south to the southern limits of the form.

Through the kindness of Dr. W. J. Breckenridge I have had the loan of specimens from Minnesota which indicate that the birds of the small group in Itasca County, in the northeastern part of the State, while intermediate toward the western form, are nearer *septentrionalis*. The same is true of material from Douglas County in north-eastern Kansas. These points serve to indicate a general border area between the eastern and western forms.

CATHARTES AURA MERIDIONALIS Swann

Cathartes aura meridionalis Swann, Syn. Accipitres, pt. 1, Sept. 28, 1921, p. 3. (Santa Marta, Province of Magdalena, Colombia.)

Cathartes aura teter Friedmann, Proc. Biol. Soc. Washington, vol. 46, Oct. 26, 1933, p. 188. (Riverside, California.)

Characters.—Edgings of the lesser wing coverts definitely darker, browner, and somewhat less in extent, so that they are less prominent than in *C. a. septentrionalis*; distal edgings and tips of secondaries averaging very slightly darker; size large, but with the maximum and average less than in *septentrionalis*.

Measurements.—Males (25 specimens), wing 487-528 (509), tail 237-268 (253), culmen from cere 22.2-26.6 (24.5), tarsus 60.6-65.1 (63.7) mm.

Females (16 specimens), wing 495-526 (511), tail 245-272 (259), culmen from cere 24.0-26.3 (25.2), tarsus 62.5-67.6 (64.9) mm.

Range.—Breeds in western North America from southern British Columbia, central Alberta, south-central Saskatchewan, and southern Manitoba south through California (except the lower Colorado River Valley) to southern Baja California, south-central Arizona, south-central New Mexico, and south-central Texas; east to south-western Minnesota, western Iowa (Audubon), and central Kansas.

Winters from California and Nebraska southward, moving in migration through Central America in vast flocks: Some continue beyond Panamá to South America from Colombia (Santa Marta; Río Guatiporí, 3,000 meters elevation, in the Sierra Nevada de Santa Marta; El Tambo, Cauca), and central Venezuela (Caicara), south to Ecuador (Monji), the Paraguayan Chaco (Orloff), and southern Brazil (Salto Grande, Rio Paranapanema, São Paulo).

Casual in Florida (Merritts Island; Cape Sable).

Remarks.—Swann, in an early review of the turkey vultures (1921, pp. 3-4) held that the birds of North America, Central America (with the exception of Isla Cozumel), and the West Indies were alike, and, therefore, listed them as *Cathartes aura aura* (Linnæus). He described the Cozumel bird as *C. a. insularis* on supposed smaller size and also separated the populations of western South America from Colombia to northern Chile and Argentina under the name of *Cathartes aura meridionalis*, which he listed as "subsp. nov. [nom. nov. *Cathartes aura aura* (Linn.) ed. 1, et auct. plur. Type loc. sugg. Colombia.]" For this he selected as type a bird in the collections of the British Museum (Natural History). This is a specimen originally in the Salvin and Godman collection, B.M. no. 87.5.1.11, ♂, taken at Santa Marta "U.S. of Colombia," by F. A. A. Simons, February 27, 1879. A label in small script, written by the collector, with ink that has faded until some words are illegible, reads in part as follows: "No. IV.I Sta Marta Sex:♂. 2 N.V. aura. Considered a great boon to the town, as they keep the place clear of all smelling meat, etc. Flesh about head fine pinky flesh color giving it the appearance from a distance of a fine red head. February 27, 1879."

On examination I have found that this type is an adult bird with light brown edgings on all the wing coverts, and the following measurements: Wing 525, tail 266, culmen from base 24.7, tarsus 66.3 mm. It is obviously a migrant from North America and as evidently one from the western part of the continent. The name *meridionalis* Swann must therefore replace the later *teter* described by Friedmann, who was the first to note that the western race was distinct. It will

be observed in the winter range of this bird as given above that I have seen another specimen of this race taken at 3,000 meters elevation in the Sierra Nevada de Santa Marta (U.S.N.M. no. 386705), in addition to others from Venezuela, Ecuador, Paraguay, and Brazil.

As indicated under *C. a. septentrionalis*, intergradation with that form in the upper Mississippi Valley is shown in birds from Minnesota where those from Dawson County in the west-central part of the State are intermediate, but are nearer *meridionalis*, as are specimens farther south from central Kansas and west-central Oklahoma (Mt. Scott, Comanche County). Allocation of the breeding birds from southeastern Kansas and eastern Oklahoma from present information is uncertain.

The diagnosis and measurements given above have been taken from birds presumed to be on or near their breeding grounds. *Cathartes a. meridionalis* shows the same cline of steadily increasing size from south to north as is found in the eastern race. To the south there is no sharp break between this form and *C. a. aura*. In fact, the type specimen of *teter* Friedmann, from Riverside, about 50 miles east of Los Angeles in southern California, is on the borderline between the two in size and color.

Occasionally, birds from arid regions taken late in summer show fading in the color of the wing coverts so that they appear lighter than normal. At first glance these may suggest *septentrionalis* but on comparison with specimens of that race in similar stage of plumage are definitely browner. First fall birds of *meridionalis*, and also of typical *aura*, often show narrow, grayish-white edgings on the middle wing coverts.

CATHARTES AURA AURA (Linnaeus)

Vultur Aura Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 86. (Veracruz, México.)

?[*Aquila*] *nudicollis* Ritter, Naturhist. Reise Westind. Insel Hayti, 1836, p. 155. ("Geyer mit nackenden Halse": No further description.)

Cathartes aura insularis Swann, Syn. Accipitres, pt. 1, Sept. 28, 1928, p. 3. (Isla Cozumel, Quintana Roo, México.)

Characters.—Similar in color to *C. a. meridionalis*, but smaller, with shorter wings and tail.

Measurements.—(Taken from birds assumed to be on or near their breeding grounds.) Males (21 specimens), wing 462-495 (478), tail 226-249 (238), culmen from cere 22.8-25.1 (22.6), tarsus 58.8-64.5 (62.4) mm.

Females (12 specimens), wing 471-495 (482), tail 231-251 (241), culmen from cere 22.7-25.9 (24.1), tarsus 58.6-66.5 (62.5) mm.

Range.—Breeds from the lower Colorado River Valley (Riverside Mountain, Calif.), southern Arizona (Yarnell, Yavapai County; Vail, Pima County; Bisbee, Cochise County), southern New Mexico (San Luis Mountains), and southern Texas (Delaware Creek; Limpia Creek; Chisos Mountains; Starr County) south into Sonora, Chihuahua, and Coahuila (southern limits on the Mexican tableland uncertain), through the Caribbean slope of tropical and subtropical México, and Central America to Honduras, probably to central Costa Rica; the Bahama Islands (Mangrove Cay, Grand Bahama, Abaco, Andros), Cuba, Isle of Pines, Jamaica, and southwestern Puerto Rico (introduced): On the mainland intergrades on the north with *C. a. meridionalis*.

In migration and winter south through Panamá to Darién (Jaqué), including the Pearl Islands (Isla San José).

Remarks.—It is evident that the division in two races, *meridionalis* and typical *aura*, appears arbitrary, with a considerable area of overlap. However, such separation seems required in view of the disparity between the populations with small size of the far south and those decidedly larger of the north, the range in the wing in males being from 462 to 525 mm. and in females from 471 to 526 mm. Smaller size is coupled with tropical and lower subtropical zone range, against the mainly Sonoran and Temperate Zone distribution of the larger, northern birds. It is probable that there are other intangible factors of difference involved that have not been evident in examination of museum specimens.

The criterion for the size limits assigned to the southern subspecies has been fixed through measurements of specimens from the resident birds of the Greater Antilles, where there is no confusion through the periodic invasion of northern migrants as is the case in the continental breeding range. The dimensions of the Antillean group then have been the yardstick used to outline the breeding range assigned to the subspecies *aura* on the mainland. Division between this group and *meridionalis* comes near the boundary between México and the United States, with the smaller southern form penetrating a short distance to the north of this line. The southern limit indicated is tentative since no specimens definitely known to be on their breeding grounds have been seen from southern Central America. I have taken winter migrants in eastern Darién so that this race may range to Colombia.

Some specimens from Cuba have the edgings on the wing coverts slightly paler than normal. It is possible that this may be due to a factor of *septentrionalis* relationship (in which this paler color is definite) from the population that is found in nearby Florida.

Immature birds in *aura*, like those of *meridionalis*, sometimes have the middle coverts edged lightly with grayish white.

CATHARTES AURA RUFICOLLIS Spix

Cathartes ruficollis Spix, Avium Spec. Nov. Brasiliam, vol. 1, 1824, p. 2. (Interior of Baía and Piauí, Brazil.)

Oenops pernigra Sharpe, Cat. Birds Brit. Mus., vol. 1, 1874, p. 26. (South bank of the River Amazon, about 100 miles above the Río Negro, Brazil.)

Cathartes aura "Illig." d'Orbigny, Voy. Amér. Mérid., vol. 4, Oiseaux, 1834, pp. 38-42, pl. 1, fig. 3. (Amérique méridionale et s'étend même dans l'Amérique du nord. Après l'avoir perdu de vue au 28.^e degré de latitude sud dans la province de Corrientes, nous ne l'avons plus retrouvé que dans la Patagonie, au 41.^e degré.)

Cathartes orbignyi Sztolcman, Ann. Mus. Polonici Hist. Nat., vol. 4, no. 3, Dec. 1, 1925, p. 322. (Based on d'Orbigny, cit. supra.)

Characters.—Definitely blacker above and below than the northern subspecies *C. a. septentrionalis*, *C. a. aura*, and *C. a. meridionalis*; under surface of body decidedly black; borders of wing coverts very dark brown, darker than in *aura*; in life, head and neck dull red, with several distinct transverse yellowish white or greenish white lines across the posterior surface of the crown and the nape; adult usually with an irregular area of yellowish white in the center of the crown.

Measurements.—Males (18 specimens), wing 476-508 (490), tail 235-265 (254, average of 17), culmen from cere 21.9-24.3 (23.2, average of 16), tarsus 60.0-64.9 (62.4, average of 17) mm.

Females (21 specimens), wing 475-509 (491), tail 235-264 (247), culmen from cere 22.3-26.6 (23.7, average of 20), tarsus 60.4-68.0 (63.8, average of 20) mm.

Range.—Throughout the tropical zone in Panamá; on the Pacific slope from near the Costa Rican boundary in western Chiriquí (including Isla Coiba, Isla Taboga, and the Archipiélago de las Perlas), and on the Caribbean side from the Canal Zone eastward; across northern Colombia (specimens seen from Córdoba, Antioquia, Bolívar, Magdalena, and Guajira); and from northern Venezuela south through South America east of the Andes to northern Argentina (Formosa, Chaco, Santa Fé), Uruguay, and southern Brazil; west to southeastern Colombia, eastern Perú, and eastern Bolivia: Northern limit in Central America uncertain, probably in Costa Rica.

Remarks.—The blacker body color, darker brown edgings on the wing coverts, and the head markings in life, where the dull red (plain in the three northern subspecies) is variegated by cross lines of yellow to whitish or greenish yellow across the back of the crown and the hindneck, with addition of an ivory-colored area in the center of the crown, readily identify this distinct race. I became familiar with the differences in plumage markings in my first observations of these turkey vultures in the field in South America, but it was not until April 1940 that I noted the interesting colors on the head in a bird taken in the foothills of the Serranía Macuire in the Guajira Peninsula, northeastern Colombia. My first report outside South America was of an immature individual shot in 1944 on Isla San José in the Gulf of Panamá, which I identified by plumage characters as *ruficollis*. At the time I believed that this bird was a wanderer from breeding grounds in Colombia. As further field work made me familiar with these vultures in Panamá, additional records have served to establish *ruficollis* as the breeding form across the isthmus on the Pacific slope from Darién on the Colombian border to the western province of Chiriquí, where I have recorded it within a few miles of the Costa Rican boundary. On the Caribbean side I have identified it from the Chagres Valley at Gamboa and Juan Mina in the Canal Zone, and in the San Blas from Mandinga, Armila, and Puerto Obaldía. The resident form to the west through the provinces of Colón and Bocas del Toro on this slope remains to be established.

There seems little doubt that *ruficollis* will be found in Costa Rica, and it may range beyond far to the north on the Pacific slope. While there are no specimens to prove this, van Rossem (1946, pp. 180-181) has reported the head color in two male turkey vultures that he shot on March 14, 1946, but did not preserve, on Isla Lechuguia (also called Isla de los Burros) off Topolobampo, northern Sinaloa, as follows: "Head, neck, cere (including encirclement of nostrils), about 'Carmine' or 'Eugenia Red'; extreme lower bare portion of neck at juncture with feather line yellowish orange, the color mostly concealed and obvious only on examination; transverse corrugations across crown between eyes and small tubercles on preocular region, ivory white; transverse corrugations of hind crown, nape, and sides of head grayish blue (about 'Deep Green-blue Gray')." Van Rossem explains that "not having a color chart at the time, the color terms in quotes are an approximation based on field notes." With this in mind, it is evident that the description is similar to the condition found in *Cathartes a. ruficollis*. The measurements that van Rossem

gives of wing, 490 and 500 mm., and of tail, 244 and 250 mm., also agree with those of that race.

Several from the Chaco of Paraguay in the Brandt collection at the University of Cincinnati are somewhat larger than the usual measurements of this race and also show lighter coloration—grayish brown to grayish white—on the outer webs of the distal ends of the secondaries. Otherwise these birds agree with *ruficollis* in blacker body color and darker coloration of the neck ruff. They appear to represent a population intermediate toward *jota* to the west. The differences are quite distinct and if found to have a broad enough distribution may warrant recognition by name. This, however, may be established only with more information, since from present data it is not certain that part or all of these larger birds may not be cold weather migrants from some Andean area to the west, and, therefore intermediates between *ruficollis* and *jota*.

In my earlier review (1926, p. 89) the name *ruficollis* was established as the proper designation for this race. Among the synonyms listed above I have examined the type of *Oenops pernigra* Sharpe in the British Museum. The specimen has an original label that states "Collected by A. R. Wallace. 1851, Upr. Amazon." Another tag reads "South bank about 100 miles above the Rio Negro." The bird is a typical example of *ruficollis*. The next name in the synonymy, *Cathartes orbigny* Sztolcman, is based, as indicated, on an account of *Cathartes aura* by d'Orbigny. While this, in part, is not specific, the head colors in the description, and in the accompanying colored plate, are those of *ruficollis*. The plate however shows three lines of prominent, rounded caruncles on the side of the neck at the base so that part of d'Orbigny's account may refer also to one of the species of the yellow-headed group.

It is of interest to observe that Azara (1802, p. 27) in his account of the Acabiráy also describes in detail the head colors of *ruficollis*.

CATHARTES AURA JOTA (Molina)

Vultur [sic] *Jota* Molina, Sagg. Stor. Nat. Chili, 1782, pp. 265, 343. (Chile.)
Cathartes occipitalis Sztolcman, Ann. Zool. Mus. Polonici, vol. 4, no. 4, Dec. 1, 1925, p. 319. (Huambo, 1,100 meters elevation, 80 kilometers southeast of Chachapoyas, Perú.)

Characters.—Secondaries margined in variable amount with light gray, in some these edgings extended to the greater coverts, and in a few to the outermost middle coverts; slightly browner above and below than *ruficollis*; size large.

Measurements.—Males (12 specimens), wing 514-546 (521), tail 252-271 (262), culmen from cere 22.6-26.1 (24.1), tarsus 62.4-71.0 (65.7) mm.

Females (6 specimens), wing 511-535 (523), tail 250-281 (260), culmen from cere 23.7-25.3 (24.4), tarsus 64.0-68.7 (66.1) mm.

Range.—From southern Colombia (where it appears to intergrade with *C. a. ruficollis*) south through the Andes, and the adjacent valleys, in Ecuador, Perú (Lago Junín), and Bolivia (Cochabamba; Choro) to southern Chile (Angol; Temuco; Puerto Montt; Estrechos de Magallanes), western and southern Argentina (Tucumán; La Rioja; western Mendoza; General Roca; Río Negro).

Remarks.—In central Colombia this form appears to intergrade with *C. a. ruficollis* to produce a bird of smaller size, and browner, less deeply black color on the body. Some specimens that come from the interior of the Chaco in northwestern Paraguay also are similar to these supposed intergrades in size and color.

Molina's description has been allocated to this interior form so that the designation by Swann (1921, p. 4) of Concepción, on the coast of Chile, as type locality is erroneous. The northern and also the eastern limits of this subspecies remain to be clearly assigned.

CATHARTES AURA FALKLANDICA (Sharpe)

Catharista falklandica Sharpe, Ann. Mag. Nat. Hist., ser. 4, vol. 11, no. 62, Feb. 1873, p. 133. (Berkeley Sound, East Falkland, Falkland Islands.)

Characters.—Similar to *C. a. jota*, but grayish edgings on wings usually more extensive; size smaller.

Measurements.—Males (5 from the Falkland Islands), wing 485-508 (499), tail 250-265 (254), culmen from cere 23.5-25.1 (24.1), tarsus 60.5-71.7 (67.1) mm.

Males (7 from coastal areas and islands, Ecuador to Chile), wing 460-507 (485), tail 220-257 (240), culmen from cere 22.7-24.8 (23.9, average of 6), tarsus 62.0-66.5 (65.3) mm.

Females (3 from Falkland Islands), wing 505-510 (508), tail 258-272 (265), culmen from cere 23.7-26.9 (24.8), tarsus 65.3-69.0 (66.8) mm.

Females (3 from islands off Ecuador and Perú), wing 466-478 (474), tail 223-225 (224), culmen from cere 23.4-25.7 (24.6), tarsus 65.5-69.6 (68.1) mm.

Range.—Falkland Islands; north along the western coast of South America to Chile (Isla Mocha, Penco), Perú (Talara, Islas de Chincha), and Ecuador (Isla Jambelí, Isla La Plata).

Remarks.—This race and *jota* are less black on the lower surface than *ruficollis*. While birds in the range outlined are similar in grayish-white markings on the wings to *jota*, and so have been included under that name by recent authors, they differ definitely in smaller size. The coastal area that they inhabit from Chile northward appears to be invaded by wandering individuals of the inland race *jota*, which has led to confusion in understanding. It may be supposed that the population is one adapted to maritime conditions influenced by colder oceanic waters.

Those found along Perú and Ecuador appear smaller than those of the Falklands and may prove separable as another form when more is known about them.

CATHARTES BURROVIANUS Cassin: Yellow-headed Turkey Vulture

Bare area of front and side of neck with numerous small papillae or caruncles, mainly low down toward the feather line, in lesser number toward the base of the head; prominent in freshly killed birds, visible in museum specimens as small, wartlike processes; hindneck feathered to base of cranium; in life, head and neck yellow and orange, varied by prominent blue markings bordered more or less with green on the crown. Color of dorsal surface dull black, with feathers tipped prominently with fuscous and fuscous-black; brownish black below; metallic bluish or greenish sheen less extensive than in the larger species with similar head colors. Development of the neck papillae begins in young birds as soon as they are on the wing.

Until I collected specimens in western Panamá in 1948, which led to the proper allocation of Cassin's ancient name *burrovianus* of 1845 (Wetmore, 1950, pp. 415-417) this species was believed to be restricted in range to South America. In the abundant material now available from the region between northeastern México and northern Argentina two geographic races distinguished by differences in size, may be recognized.

CATHARTES BURROVIANUS BURROVIANUS Cassin

Cathartes Burrovianus Cassin, Proc. Acad. Nat. Sci. Philadelphia, vol. 2, no. 8, March-April 1845, p. 212. (Near Veracruz, Veracruz, México.)

Size small; wing 432 to 459 mm.

Measurements.—Males (10 specimens), wing 432-455 (445.4), tail 195-225 (207.2), culmen from cere 19.6-23.3 (21.3), tarsus 51.1-59.1 (57.1), approximate width of central rectrix 42-49 (46.3) mm.

Females (12 specimens), wing 444-459 (449.3), tail 193-230 (206.8), culmen from cere 21.2-24.0 (22.1), tarsus 56.2-60.0 (58.0), approximate width of central rectrix 43-49 (46.3) mm.

Range.—Eastern México, in Tamaulipas (Tampico; Lomas del Real), Veracruz (Veracruz; Alvarado), and Tabasco (Miramar; Villa Hermosa); British Honduras (Belize); Honduras (Puerto Lampira); Pacific slope of Panamá from Chiriquí (David) through Veraguas (Soná), Coclé (Río Hato; Antón), Herrera (El Rincón; Pesé; Santa María), and Los Santos (Pedasí) to eastern Province of Panamá (La Jagua; Río Chico); Colombia from Atlántico, Magdalena (Santa Marta; Gaira), and Guajira (Maicao) south locally to the upper Río Cauca, upper Patía Valley in Cauca, the upper Magdalena Valley in Huila, and, in the northern llanos, to northern Meta (Quenane); northwestern Venezuela, in Zulia (Encontrados) and Falcón (El Planchón).

There is some seasonal variation in depth of color of the head. An adult female near breeding stage shot on March 24, 1961, at La Jagua, Panamá, had the iris orange-red; center of the crown indigo, in an irregular triangle with the apex forward and the base behind, bordered narrowly on either side by pale greenish blue; side of head, including the loreal area and the base of the mandibular rami, bright orange; the bare foreneck, including the prominent caruncles, dull orange; back of the head dull blue, crossed by three irregular rows of caruncles which are dull orange; bill dull ivory white; crus dull yellowish white; front of tarsus dull greenish gray, rest dull white; toes fuscous black; claws fuscous. In another female, also adult but in resting stage, taken at the Ciénaga Macana, Herrera, March 17, 1948, the iris was red; center of crown and spot in front of the eye dull bluish gray; cere, forepart of crown to center of eyes, nape, back of head, and neck to throat dull orange-red; lores greenish yellow; sides of head from posterior loreal space back around the eye and ear, including the area below the gape, bright orange. A companion bird taken at the same time was slightly duller.

In México and Central America the yellow-headed vulture tends to frequent lowland marshy areas that often are difficult of access. As it is far less common than the red-headed turkey vulture, found everywhere, it may be overlooked since the two are closely similar except in the head color, which is seen only under favorable conditions. Now that attention has been attracted there have been recent reports that have added considerably to the details of range. Dr. and Mrs. Richard R. Graber (1954, pp. 165-166) collected one on July 21,

1953, in Tamaulipas, 8 miles north of Tampico. They recorded others in this general area south of Altamira, and one earlier, on June 19, at Lomas del Real, 30 miles north of Tampico, near the Gulf of México. Recently Col. L. R. Wolfe has sent me the skin of an immature bird taken on March 23, 1964, 18 miles south of Alvarado, in Veracruz.

Specimens lent to me by Dr. George H. Lowery, Jr., from the Museum of Zoology, Louisiana State University, include five from Teapa, Miramar, and Villahermosa, Tabasco, taken in 1959 and 1960; one from Belize, British Honduras, August 26, 1960; and two from Puerto Lampira, Honduras, February 5, 1963. In my work in Panamá I have found the yellow-headed vulture in the lowlands of the Pacific slope from near the Costa Rican boundary to the Province of Panamá near the mouth of the Río Bayano, 25 miles east of the Canal Zone.

In view of the known occurrence of these birds in southern Tamaulipas the possibility that they may range farther north should be kept in mind. In the early period when the identity of Cassin's *Cathartes burrovianus* was not clear Dresser (1865, pp. 322-323) reported a small vulture seen near Brownsville, Tex., that he thought might be this species, but to date there has been no record of it.

The outline of the range of this race in Colombia is taken mainly from discussion by Lehmann and Dugand. Personally I have examined specimens from Bolívar (Simití), Atlántico (Laguna de Guájaro), northern Magdalena (Santa Marta), and Guajira (Maicao).

CATHARTES BURROVIANUS URUBITINGA Pelzeln

Cathartes Urubitinga Pelzeln, Sitzungsab. math.-naturw. Kl. Akad. Wiss. Wien, vol. 44, pt. 1, 1861, p. 7. (Forte do Rio Branco = Forte São Joaquim, Rio Branco, Brazil.)

Cathartes burrovianus dugandi Lehmann, Mus. Hist. Nat. Univ. Cauca Nov. Colombianas, no. 3, Dec. 1, 1957, p. 120. (Caicara, Bolívar, Venezuela.)

Larger, wing 457-509 mm.

Measurements.—Males (27 specimens), wing 457-502 (475.6), tail 205-238 (216.0), culmen from cere 20.5-24.7 (21.9, average of 25), tarsus 56.5-68.8 (60.8), approximate width of middle rectrix 43-50 (46.9) mm.

Females (18 specimens), wing 461-509 (484), tail 204-236 (219), culmen from cere 20.8-23.4 (20.7, average of 17), tarsus 53.2-64.0 (60.0), approximate width of middle rectrix 43-51 (46.2, average of 13) mm.

Range.—From the llanos of southeastern Colombia, central and eastern Venezuela (Caicara, Bolívar; Cantaura, Anzoátegui), British Guiana (Abary, Georgetown), and Surinam (near Paramaribo) through Brazil and Paraguay to northern Argentina (Las Palmas, Chaco; Mocoví, Santa Fé), and Uruguay.

An adult male that I collected on July 20, 1920, near Las Palmas, Chaco, in northern Argentina, had the iris red; side of the head and throat deep chrome yellow shading to olive-buff at base of bill; center of crown dark blue bordered on either side by dark green; a spot of dull slate blue beneath the nostrils; rest of bill cream buff; tarsus cartridge buff, shading to neutral gray on the toes.

Division of this species into two geographic races necessarily is arbitrary since the measurements on which this is based show a cline from the smaller birds of Central America, northern Colombia, and northwestern Venezuela to the larger birds of the rest of South America. This seems justified, however, by the uniformity found within the limits assigned to each group, with a considerable difference between the smaller birds of the north and the larger ones of South America.

The yellow-headed vulture was first reported in Colombia by F. Carlos Lehmann (1940, p. 461) under the name Guala de Cabeza Amarillo, *Cathartes urubitinga* Pelzeln, with specimens listed from Vaupés and Valle del Cauca. In April 1941, in the Guajira Peninsula, Dr. Lehmann and I collected specimens of the yellowhead near Maicao (preserved by Lehmann) and later in April and early May, I saw them near Uribia, Nazaret, and Puerto Estrella. Dugand (1941, p. 54) listed additional records, based in part on specimens and observations by Dr. Lehmann that included the birds from Maicao.

In another account Lehmann (1944, pp. 187-190) gave further details of occurrence that included the presence of these birds at an elevation of 900 meters in the upper valley of the Río Patía, south of Popayán, a stream that flows through Nariño to the Pacific Ocean, and also reported these birds near Cali in the Department of Valle. He noted that they frequented marshy areas and that their main food was fish. In a further paper Dugand (1951, pp. 1-4) noted differences in size and listed the birds as two species under the names *burrovianus* and *urubitinga*. The following year Dugand (1952, pp. 1-4) discussed the question again and treated the two as geographic races of *burrovianus*. It should be noted that in his account and list of material examined some of the specimens were wrongly

identified, as I have found that specimens under *urubitinga* include several *Cathartes aura ruficollis*. Part of his larger birds were the species that is described beyond. Lehmann (1957, pp. 118-121) gave a summary with further details divided under the two subspecies, and in this proposed to separate the two by a third race that he named *Cathartes burrovianus dugandi*, with the type a female in the American Museum of Natural History from Caicara, Bolívar, Venezuela. With recognition of only two races in this species, this name falls under *C. b. urubitinga*.

In June 1954, through the kind attention of Dr. G. Rokitansky I had the opportunity to examine Pelzeln's type material in the Naturhistorisches Museum in Vienna. The specimens in the series include three adult and two immature birds collected by Joh. Natterer between 1817 and 1835. Though at one time four of these specimens had been mounted for exhibition, all were in a fair state of preservation when their age as museum specimens is considered. Three, an adult male, adult female, and one of the immature birds, are labeled from "Forte do Rio Branco, Nord-Bras.," a locality that corresponds to Forte São Joaquim, Rio Branco, in modern Brazil. This is accepted above as the type locality since the others are marked only "Brasilien," as is an adult cotype in the U.S. National Museum, one of the original specimens studied by Pelzeln, received in exchange and entered in our catalog in 1864. My notes on the entire series fully substantiate the name *urubitinga* as applicable to the yellow-headed turkey vulture and to its southern race.

CATHARTES MELAMBROTUS sp.nov.: Greater Yellow-headed Vulture.

Characters.—With prominent caruncles on the neck, and head color, as in *Cathartes burrovianus* Cassin, but size definitely larger; tail decidedly longer with broader rectrices, the central pair especially much wider; plumage entirely deep black with greenish and purplish sheen, without mixture of brown in the wing coverts, or elsewhere.

Description.—Type, U.S.N.M. no. 483532, male (fully adult), collected by Pinney Schiffer at Kartabo, British Guiana, January 15, 1930. Plumage deep black throughout, with an iridescent sheen, greenish in the main, but in part dull bluish with the light at certain angles; under surface of wings and tail dull dark brownish gray; concealed down pure white.

Measurements.—Males (9 specimens), wing 488-530 (505.7, average of 8); tail 252-275 (264.4); culmen from cere 23.2-26.2 (24.6,

average of 8) ; tarsus 68.5-75.1 (70.7) ; approximate width of central rectrix 59-70 (63.4) mm.

Females (3 specimens), wing 510-512 (511, average of 2) ; tail 272-285 (279), culmen from cere 23.9-25.5 (24.6), tarsus 69.3-72.5 (70.9) ; approximate width of central rectrix 60-67 (64.3) mm.

Type, male, wing 508, tail 272, culmen from cere 26.2, tarsus 68.5, approximate width of central rectrix 63 mm.

A color photograph of a recently killed adult male, taken by John P. O'Neill at Tingo María, Perú, July 1, 1962, shows clearly that the iris was red ; bill flesh color ; side of the head and throat deep yellow to light orange ; and the crown and a spot in front of the eye deep blue.

Range.—From southeastern Colombia (Río Vaupés), the Río Orinoco in southern and eastern Venezuela (Isla Corocoro, Amazonas ; Piacoa, Delta Amacuro), British Guiana (Kartabo ; Rockstone ; Kamakuna), and Surinam (Keiserberg Airstrip ; Wilhelmina Mountains), to eastern Perú (Río Curanjá, Loreto ; Tingo María, Huánuco) and central Pará in northern Brazil (Tauary on the Rio Tapajós ; Tapara on the Rio Xingú).

Remarks.—As my studies of specimens of the yellow-headed vultures progressed it became evident that there were occasional specimens that did not agree with the usual pattern of *Cathartes burrovianus* in size and color. In fact, certain birds were definitely troublesome in attempts to outline characters under which this species could be recognized. The first of these aberrant individuals was a skin in the American Museum of Natural History, an adult female of unknown locality that had died in captivity at the New York Zoological Society zoo on December 23, 1918. Presently I saw another of similar form in the Museum of Comparative Zoology, and later others in the Chicago Natural History Museum. At first I supposed that these might be the bird described briefly by Sharpe (1874, p. 26) as *Oenops pernigra*, but in due course when I saw this type it proved to be an individual of *Cathartes aura ruficollis*. There remained the possibility then that they were *Cathartes urubitinga*, named by Pelzeln from northern Brazil, but when I visited the Naturhistorisches Museum in Vienna I found that the type series were all individuals with duller color of *burrovianus*, and with the size of the southern population of that species listed above under Pelzeln's name as *Cathartes burrovianus urubitinga*. It became obvious then that the larger birds represented a distinct group that has been overlooked. Since their known range is included within that of *C. b. urubitinga* they must be regarded as a distinct species.

For the extension of range to eastern Perú I am indebted to John P. O'Neill and Dr. George H. Lowery, Jr. It is probable that this species ranges also to northeastern Bolivia.

KEY TO THE SPECIES OF THE GENUS CATHARTES

1. Bare skin of the side and front of the neck at the base smooth; upper hind-neck in adult not feathered; bare skin of head and upper neck in adult birds in life dull red, usually plain, but in the subspecies *ruficollis* with several narrow lines of yellowish or greenish white across the back of the cranium. *Cathartes aura*
 Bare skin of the side and front of the neck at the base with numerous caruncles, prominent in life; in museum specimens visible as small, wart-like projections; hindneck in adult feathered to near the base of the cranium; bare skin of head and upper neck in adult birds in life yellow and orange varied by markings of blue. 2
 2. Back and wings with many feathers tipped and edged prominently with dull grayish brown; under surface more brownish black; definitely smaller, with tail shorter, not more than 240 mm. long; rectrices, especially the central pair, less than 52 mm. wide. *Cathartes burrovianus*
 Plumage deep black throughout, with prominent greenish or bluish reflections; decidedly larger, with tail longer, 250 to 280 mm. or more; rectrices, especially the central pair, 59-70 mm. wide. . . . *Cathartes melambrotus* sp. nov.
- Details of the characters that mark subspecies are given in the main text.

LITERATURE CITED

AZARA, FELIX DE

1802. Apuntamientos para la historia natural de los páxaros del Paraguay y Rio de la Plata. Vol. 1, pp. i-xx, 1-534.

DRESSER, H. E.

1865. Notes on the birds of southern Texas. Ibis, n.s., vol. 1, no. 3, July, pp. 312-330.

DUGAND, ARMANDO

1941. Adiciones a la lista de aves conocidas en Colombia. Caldasia, no. 3, Dec. 15, pp. 53-61.

1951. Descubrimiento de *Cathartes burrovianus* Cassin en Colombia. Rev. Acad. Colombiana Cienc. Exact. Fís. Nat., vol. 8, no. 30, April, pp. 154-156.

1952. Observaciones adicionales sobre *Cathartes burrovianus* y *Cathartes urubitinga*. Lozania (Act. Zool. Colombiana), no. 2, June 30, pp. 1-4.

GRABER, RICHARD R., and GRABER, JEAN W.

1954. Yellow-headed vulture in Tamaulipas, México. Condor, vol. 56, no. 3, May 21, pp. 165-166.

LEHMANN V., F. CARLOS

1940. Contribución al estudio y conocimiento de las aves rapaces de Colombia. Rev. Acad. Colombiana Cienc. Exact. Fis. Nat., vol. 3, no. 12, May-August, pp. 455-461, 2 pls.
1944. Distribución de *Cathartes urubitinga* en Colombia. Rev. Univ. del Cauca, no. 3, March-April, pp. 187-190, 1 pl.
1957. Contribuciones al estudio de la fauna Colombiana XII. Mus. Hist. Nat. Univ. Cauca Nov. Colombianas, no. 3, Dec. 1, pp. 101-156.

SHARPE, R. BOWDLER

1874. Catalogue of the birds in the British Museum. Vol. 1, pp. I-XIV, 1-480, 14 pls. (col.)

SWANN, H. KIRKE

1921. A synopsis of the Accipitres (diurnal birds of prey), Part I, *Vultur* to *Accipiter*, Sept. 28, pp. 1-63.

VAN ROSSEM, A. J.

1946. Notes on distribution and color of the Mexican turkey vulture. Condor, vol. 48, no. 4, July 31, pp. 180-181.

WETMORE, ALEXANDER

1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. U.S. Nat. Mus. Bull. 133, Feb. 1, pp. I-IV, 1-448, 20 pls.
1950. The identity of the American vulture described as *Cathartes burrovianus* by Cassin. Journ. Washington Acad. Sci., vol. 40, no. 12, Dec. 15, pp. 415-417.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NUMBER 7
(END OF VOLUME)

Mary Vaux Walcott Fund for
Publications in Botany

A NEW SPECIES OF MARINE PENNATE
DIATOM FROM
HONOLULU HARBOR

By

PAUL S. CONGER

Associate Curator, Division of Cryptogams
Department of Botany, Smithsonian Institution



(PUBLICATION 4593)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 23, 1964

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 146, NUMBER 7
(END OF VOLUME)

**Mary Vaux Walcott Fund for
Publications in Botany**

A NEW SPECIES OF MARINE PENNATE
DIATOM FROM
HONOLULU HARBOR

By
PAUL S. CONGER
Associate Curator, Division of Cryptogams
Department of Botany, Smithsonian Institution



(PUBLICATION 4593)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 23, 1964

PORT CITY PRESS, INC.
BALTIMORE, MD., U. S. A.

Mary Vaux Walcott Fund for
Publications in Botany

A NEW SPECIES OF MARINE PENNATE
DIATOM FROM HONOLULU HARBOR

By PAUL S. CONGER

*Associate Curator, Division of Cryptogams
Department of Botany
Smithsonian Institution*

(WITH ONE PLATE)

A RATHER DISTINCTIVE and interesting marine benthic epiphytic diatom from the bottom of Honolulu Harbor, Hawaii, was collected by Dr. R. E. Johannes of the Department of Zoology, University of Hawaii, and isolated and cultured by him for use in investigations on phosphorus metabolism, and as a source of food for amphipods which were being used experimentally. He submitted it to me for identification, and I am indebted to him for bringing it to my attention. I am also indebted to Dr. David L. Correll, of the Division of Radiation and Organisms of the Smithsonian Institution, for carrying the diatom in culture for a few weeks. I required access to adequate fresh supplies for this study, because the diatom proved too delicate to allow satisfactory permanent preparations to be made.

The diatom cultures well, multiplies rapidly, and is very hardy in artificial seawater culture medium. For these reasons it should be a very good species for investigational purposes and a good experimental form for wider use. Whether it will continue to thrive and can be maintained indefinitely away from supplies of fresh seawater remains to be seen. For all their hardness under good conditions, these forms are very sensitive and demanding.

It would also be desirable to make electron micrographic studies of it to determine its more intricate and finer structure, but I have not been in a position to do this. Because of the very great delicacy of the shell, the structure is not readily seen with the optical microscope. For this reason the electron micrographic studies would be helpful in its identification.

Although it is not a particularly diminutive form in general dimensions, it is one of the most delicate ones I have had occasion to study. I have given it the name *subhyalina* to indicate its extremely tenuous and gossamer character.

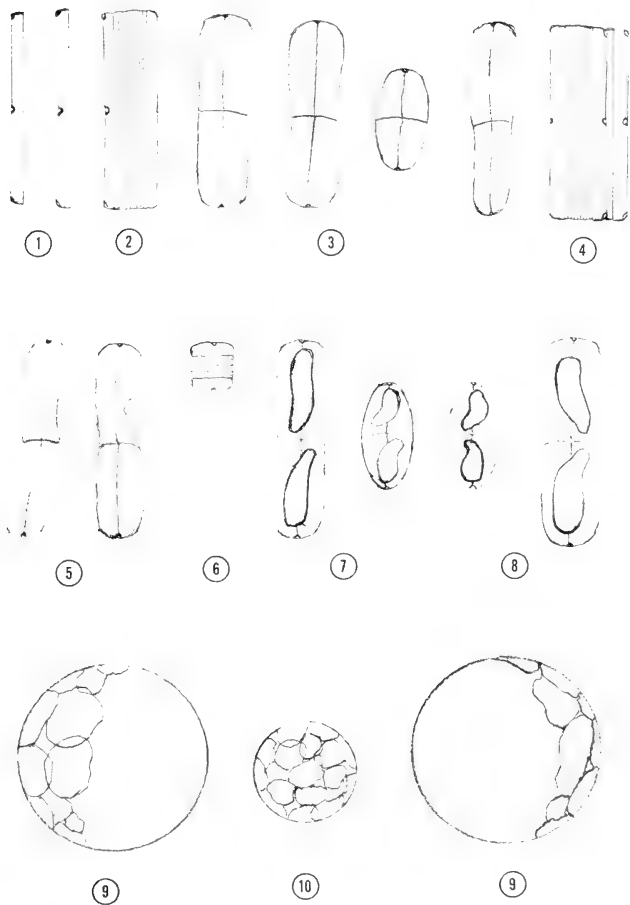
ACHNANTHES SUBHYALINA Conger, sp. nov.

Plantae unicellulares; valvae breves breviter oblongae vel lineari-oblongae, interdum paullo apice constrictis, 5-10 μ longae, 3-4 μ latae, apice late rotundatae; valva superior cum pseudoraphe angustissima, recta, mediam valvae occupante, cum linea mediana transversa angustissima, nodulis terminalibus et nodulo centrali indeterminato, tota superficie valvae hyalina; valva inferior similis; chromatophori brunnei, pyriformes, alterni vel oppositi.

Habitat: In seawater of Honolulu Harbor, Hawaii, originally collected by R. E. Johannes.

Frustules short- to linear-oblong, or long-rectangular with rounded ends, the latter type sometimes slightly, almost imperceptibly, constricted in face (valve) view; girdle view rectangular with rather sharp (or scarcely rounded) corners; valve surface flat and straight apically, sometimes slightly depressed in the center; valve mantle narrow, girdle zone two to six times as wide as valve mantle, with a lined appearance as if comprised of intercalary bands; end view of frustule square-rectangular with rounded corners; valve surface mildly convex transapically, with rounded margins; raphe a straight narrow line; valve with a median, narrow, transapical groove crossing it at right angles to raphe, in girdle aspect the groove, due to focal-depth refraction, with the appearance of a triangular or cone-shaped bright spot resembling a central nodule (believed a false optical effect); the slightly thickened corners of the valve end with the impression of terminal nodules in girdle view; valve surface markings cannot be resolved with the optical microscope. Valves 5-10 μ long, 3-4 μ wide.

Chromatophores in young, actively growing cells are bright orange-brown, more or less "tear-" or "pear-shaped," with truncate ends, one in each end of the cell, with narrow ends toward the cell center, characteristically alternate, much less frequently opposed (that is, on the same side), occupying (estimated) one-third to one-half the cell volume, the alternate arrangement giving frequently a twisting, sigmoid, scolio, or amphipruroid effect (actually not present). In older cells, the chromatin material is either duller, darker brown, or paler, and occupies more of the cell volume in a somewhat irregular pattern, but



Achnanthes subhyalina, sp. nov.

(1) Single valves (girdle view); (2) complete frustule (girdle view); (3) valves (face view); (4) frustule (girdle view) with extra attached valve, sometimes seen; (5) abnormal valves; (6) end view of one frustule; (7) frustules (valve view) with chromatophores alternately arranged; (8) same, with chromatophores oppositely arranged; (9) spherical "resting" spore bodies with peripheral chromatin masses; (10) same completely filled by chromatin masses.



always leaves a central (transapical) stauros-like area, in both valve and girdle aspect.

The shells are exceedingly delicate and gossamer-like and are not amenable to conventional microscopic preparation; they disappear completely in strong acid but withstand dilute hydrochloric and sulfuric acids, which turn the chromatin material green but do not digest it. The cells are very slightly silicified and are destroyed by incineration. No mounting is possible by conventional methods.

The vegetative cell population contains occasional spherical, transparent bodies, peripherally pigmented with dense, essentially round, but more or less irregular, pigment masses over a quarter or less of the periphery of the sphere; the remainder of the cell is clear. The diameters of these spherical bodies range in size from about the length of the frustules to up to twice this length. Occasionally the whole sphere is filled with peripheral pigment bodies, obviously chromatin material similar to that of the diatoms, although no "shell" forms are distinguishable, or if present are collapsed. These pigment masses appear to be either residues of former cells or perhaps parts of potential ones. They become quite numerous in old, stagnant, decadent cultures. (Whether they are "auxospores," or some reproductive phase, or a protective or degradational resting body in senile and decadent cultures I am unprepared to conclude.)

The cells are actively motile in new and healthy cultures, moving in a mostly linear course, with few reversals; the movement in a reversed direction is short (usually less than a cell length) before forward motion is again resumed. The rate of movement is about five to eight times the cell length in a minute. The cells in aging cultures, even though they may appear otherwise healthy, are slower, moving little or but a cell's length in a longer time.

The cells are very strongly adhesive to the substrate in an Erlenmeyer flask culture, making an even brown coating on the bottom of the flask, and require somewhat violent shaking to loosen them; in contrast, for instance, with *Phaeodactylum tricorutum*, which is either nonadhesive or readily stirred. Once detached from the substrate, they quickly form in dark brownish, free-floating aggregates or clumps that never adhere again to the bottom, but adhere strongly to one another.

This diatom is probably one that migrates in its natural benthic environment in response to diurnal illumination, although there is no observational evidence of this.

In young, healthy cultures among large populations there are no

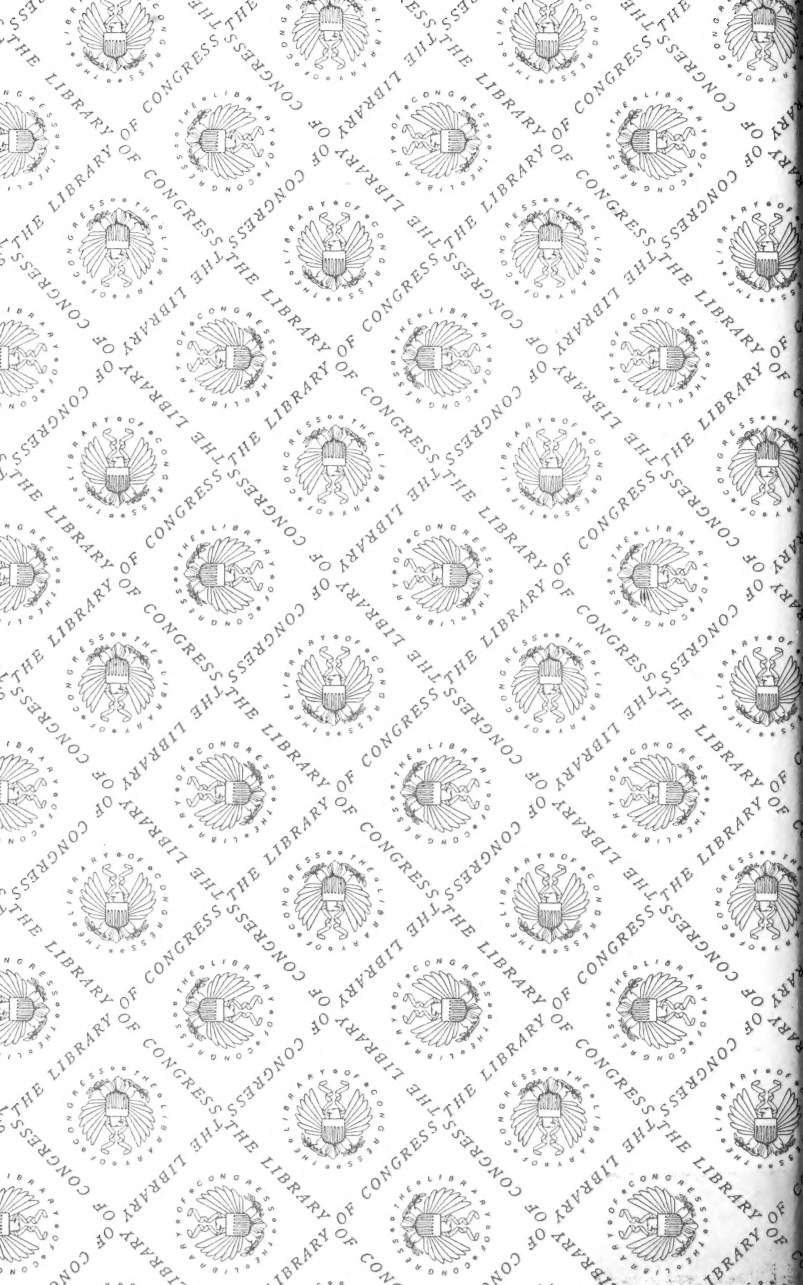
empty, "dead" cells (unpigmented frustules), which is the only condition in which they could be examined morphologically at all adequately. In quite old cultures, empty frustules, and occasionally separate valves, become more frequent. Empty frustules or valves are dim-whitish in appearance and almost invisible in water. This "whitish" appearance of the diatom in water under ordinary full-field illumination suggests the advantage of "dark-field" illumination and, indeed, the latter (or "phase-contrast") is a good way to bring out more prominently the obscure cell features. The diatoms are most readily located by the much greater visibility, in girdle view, of the false "central nodule" which can be picked up as a bright triangular spot, from which the rest of the cell outline can then be followed. Were it not for this the shells would not be easy to make out or would be overlooked completely. In valve aspect the raphe and transapical groove are the more easily seen features, appearing as moderately bright white lines.

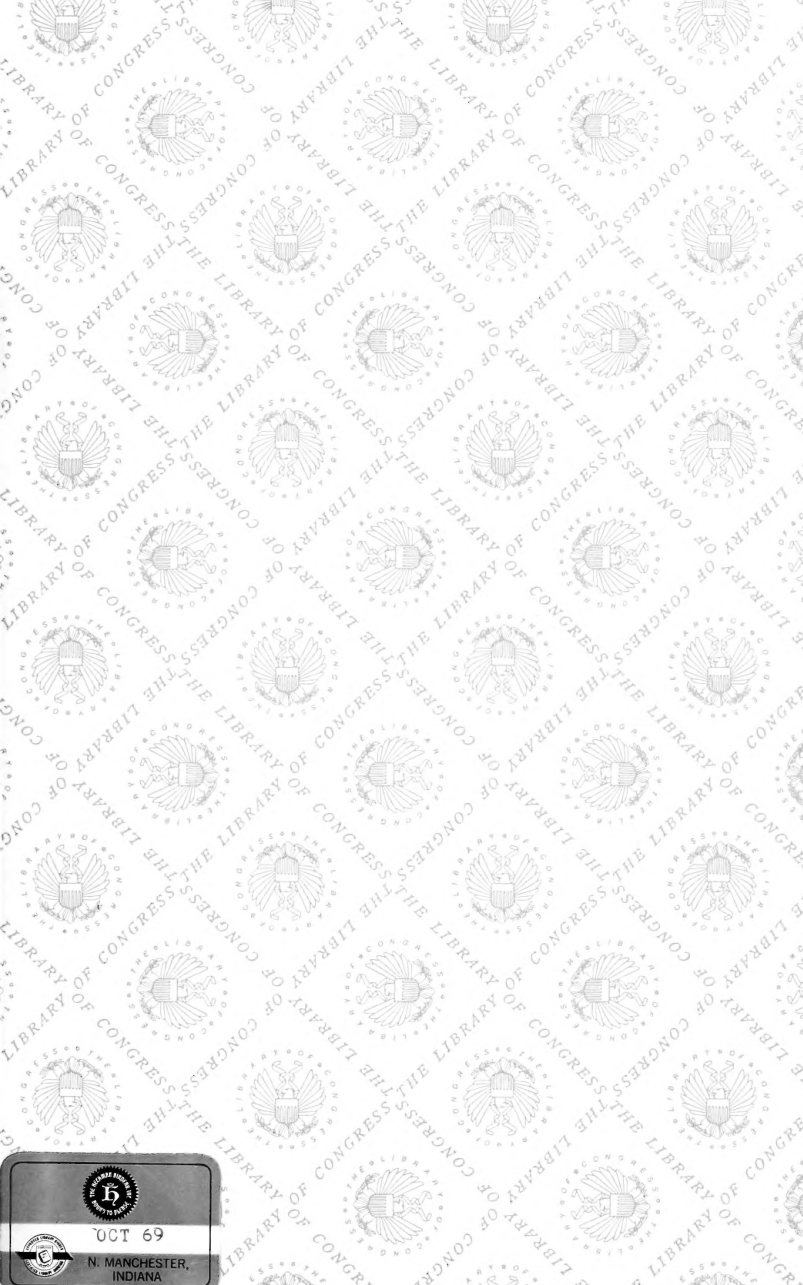
Although this diatom is necessarily described on fewer structural features than usual, it is felt that it should be readily identifiable from these features, and by the very characteristic "tear-" or "pear-shaped," alternately arranged chromatophores, which afford it a rather conspicuous and distinctive character. I have not been able to secure a separate view of the inferior valve, and so that has been hypothecated from the girdle view of the whole frustule.

There is difficulty and uncertainty in making out even the generic status, although the diatom character is immediately evident and not at all to be questioned. The prevalence, range, and frequency of *Achnanthes subhyalina* are not likely soon to be determined. Its small size, frailty, and general obscurity make it a form not likely to be found by the conventional methods of examination of natural materials that account for the discovery of most species of diatoms. It is unlikely to be found except when in quantity in isolated cultures, which suggests that there may well be many other such diminutive forms that have escaped notice due to the limitations of conventional procedures. On the other hand, the readiness and rapidity with which it grows and its evident hardness suggest that it may be a widely distributed and abundant species. Because of its frailty and low degree of silicification, the shells are not likely to persist after death in the natural environment or to be recognized if they do persist. It must be observed in the living state for determination or recognized from dead shells in culture material. By present methods no permanent preserved "type" preparations, such as microscope slides, have

been possible. Material preserved in formalin, alcohol, or other liquid preservative is of uncertain and doubtful value. The living culture may best serve as confirmatory or "type" material.

In the active, healthy cultures there is some range in the size and shape of the cells, and the size, shape, and arrangement of the chromatophores, but this is well within the limits of expectation. In the large numbers of specimens observed the growth pattern is very consistent and typical, and the incidence of distorted or otherwise abnormal forms is exceedingly low. The generally healthy vigor of the species implies that it thrives under cultural conditions and adapts readily to them. The adaptability suggests it as a dependable and useful culture organism for many experimental purposes. The discovery of *Achnanthes subhyalina* suggests the importance of widespread "culturing" as a valuable exploratory method, as yet meagerly employed, for the recognition of many minute, obscure, and transient forms which have so far eluded detection and may continue to do so in the future without this method. It is more and more recognized that these watery, next to invisible, transitory forms may comprise a substantial, functionally important constituent of the micropopulation of the ocean. Hitherto they were a "blindspot" in our studies, which cannot afford to be overlooked any longer. They will be, at best, a tedious, difficult, and special study.





OCT 69

N. MANCHESTER,
INDIANA

100